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SOCIETE ROYALE BELGE DE MALACOLOGIE

Description of new genera and new species of Ergalataxinae (Gastropoda: Muricidae)

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KEYWORDS. New taxa, Gastropoda, Muricidae, Ergalataxinae, Indo-Pacific, South Atlantic.

ABSTRACT. The recent genetic analysis of the muricid subfamily Ergalataxinae has led to a better understanding of this subfamily, but some species were left without appropriate generic assignments and the classification of others required revision. This knowledge gap is partially filled herein, with new combinations and the description of three new genera. The examination of new material, along with a careful re-examination of and comparison to existing material, resulted also in the identification of nine new species. These new genera and new species are described herein, lectotypes are designated and new combinations are given. The geographical range of all the new species is provided on maps. All new species are compared with related or similar species. The radula of *Morula palmeri* Powell, 1967 is illustrated for the first time.
New genera: *Claremontiella* n. gen., type species *Purpura nodulosa* C.B. Adams, 1845; *Murichorda* n. gen., type species *Purpura fiscellum* Gmelin, 1791; *Lauta* n. gen., type species *Ricinula parva* Reeve, 1846.
New species: *Cytharomorula arta* n. sp. from Reunion Island; *C. absidata* n. sp. from New Caledonia; C. *elegantula* n. sp. from the western Pacific Ocean; *C. fatuhivaensis* n. sp. from the Marquesas; *C. manusuduirauti* n. sp. from the Philippines; *Orania pseudopacifica* n. sp. from the Marquesas; *Tenguella chinoi* n. sp. from the eastern Indian and western Pacific Oceans; *T. ericius* n. sp. and *T. chinoi* from the western Pacific Ocean; and *Claremontiella adiakritos* n. sp. from western Mexico. *Claremontiella adiakritos* n. sp. was previously confused with *Ricinula ferruginosa* Reeve, 1846, a species which has been combined with *Morula*, *Evokesia* and *Pascula*, and which is a synonym of *C. nodulosa* (C.B. Adams, 1845).
Lectotypes are designated for *Fusus pachyrhaphe* E.A. Smith, 1879 (= *Orania pachyrhaphe*) and *Purpura granulata* Duclos, 1832 (= *Tenguella granulata*).
New combinations: *Morula nodulosa* (C.B. Adams, 1845) and *Morula consanguinea* (E.A. Smith, 1891) are transferred to *Claremontiella* n. gen.; *Orania ornamentata* Houart, 1995 is transferred to *Cytharomorula*; *Morula parva* (Reeve, 1846) is transferred to *Lauta* n. gen.; *Muricodrupa fiscellum* (Gmelin, 1791), *Morula rumphiusi* Houart, 1996 and *Muricodrupa jacobsini* Emerson & D'Attilio, 1985 are transferred to *Murichorda* n. gen.; *Morula anaxares* (Kiener, 1835) is transferred to *Muricodrupa*; *Muricopsis carnicolor* Bozzetti, 2009 and *Morula taiwana* Lai & Jung, 2012 are transferred to *Orania*; and *Morula palmeri* Powell, 1967 is transferred to *Pascula*. *Cantharus albozonatus* E.A. Smith, 1890 is removed from *Orania*, to which it was assigned in WoRMS (MolluscaBase 2018), and transferred to the genus *Enginella* Monterosato, 1917 (Buccinoidea, Pisaniidae).
New synonymy: *Sistrum ventricosulum* G. & H. Nevill, 1875 is considered synonym of *Morula echinata* (Reeve, 1846).

INTRODUCTION

Four species were originally assigned to the subfamily Ergalataxinae (Gastropoda, Muricidae): *Bedevina birileffi* (Lischke, 1871), *Ergalatax contracta* (Reeve, 1846), *E. tokugawai* Kuroda & Habe, 1971 and *Cytharomorula vexillum* Kuroda, 1953. The subfamily diagnosis was based on morphological characters of the shell, radula and egg capsule (Kuroda et al. 1971). Later on, many genera

and species were added to the subfamily, counting now 20 genera and 146 species recognized as valid (WORMS). Recent molecular genetic analyses confirmed the validity of this subfamily within the Muricidae (Barco et al. 2010; Claremont et al. 2008; Claremont et al. 2013).

Claremont et al. (2013) analysed 52 ergalataxine species in 18 genera, representing 36% of the currently accepted species and 90% of the genera, and showed that many of the currently accepted genera were polyphyletic, thus requiring further analysis. In addition, some of the species included by Claremont et al. (2013) were unidentified, and potentially represented new species. To address some of these issues, we herein discuss and clarify the taxonomy of the genera *Muricodrupa* Iredale, 1918, *Cytharomorula* Kuroda, 1953, *Orania* Pallary, 1900, *Pascula* Dall, 1908, and *Tenguella* Arakawa, 1965. In addition, three new genera are described, together with several new species in *Cytharomorula*, *Orania*, *Pascula*, *Tenguella* and *Claremontiella* n. gen. Our conclusions are based on the results from Claremont et al 2013, completed by the examination of additional material, including newly sequenced samples.

Material and methods

Material

The material studied here primarily includes specimens collected on various cruises conducted by the MNHN/IRD in the Indo-West Pacific. Other specimens were from the collections of the Natural History Museum, United Kingdom; the KwaZulu-Natal Museum, South Africa; the Houston Museum of Natural History, Houston, Texas, U.S.A; and the personal collection of the first author.

Specimens from the following expeditions of the MNHN/IRD were examined: BENTHEDI: Mayotte, northern Madagascar, Mozambique Channel, 1977; MD32: Reunion Island, 1982; BIOCAL: New Caledonia, 1985; CHALCAL 2: New Caledonia, 1986; SMIB 3: New Caledonia, 1987; SMIB 4: New Caledonia, 1989; SMIB 5: New Caledonia, 1989; BERYX 11: New Caledonia, 1992; MUSORSTOM 7: SW Pacific, Wallis & Futuna, 1992; SMIB 8: New Caledonia, 1993; BATHUS 2: New Caledonia, 1993; MUSORSTOM 8: Vanuatu, 1994; MUSORSTOM 9: Marquesas, 1997; LIFOU 2000: New Caledonia, 2000; BORDAU 2: Tonga, 2000; NORFOLK 1: New Caledonia, 2001; NORFOLK 2: New Caledonia, 2003; PANGLAO 2004 and 2005: Philippines; EBISCO: New Caledonia, 2005; SANTO 2006: Vanuatu, 2006; AURORA 2007: Philippines; TERRASSES: New Caledonia, 2008; MAINBAZA: Mozambique, 2009; MIRIKY: Madagascar, 2009; ATIMO VATAE: Madagascar, 2010; EXBODI: New Caledonia, 2011; PAPUA NIUGINI: Papua New Guinea, 2012; PAKAIHI I TE MOANA: Marquesas, 2012; KANACONO: New Caledonia, 2016; KANADEEP: New Caledonia, 2017; MD208: Walters Shoal, south of Madagascar, 2017 and BIOMAGLO: Mayotte, Glorieuses and Comoros islands, 2017.

The material used for the phylogenetic tree is listed in Table 1

Morphological analyses

The characters used to describe shell morphology address the general aspect of the shell, its shape, size, and colour, the shape of the spire including the number and features of the protoconch and teleoconch whorls, details of the suture and of the subsutural ramp, details of axial and spiral sculpture, the aperture, the siphonal canal, and when available, the characters of the operculum and radula.

The method used to determine diameter and height, and to count the number of protoconch whorls, follows Bouchet & Kantor (2004) as shown in Fig. 1. The morphology of the radula is described starting from the rachidian tooth, followed by the lateral teeth (Fig. 2). Unless otherwise indicated, species descriptions are based on the holotype and the paratypes. The bathymetric ranges given herein are the inner values of the recorded depths: the deepest minimum and the shallowest maximum of each recorded depth range.

Molecular analyses

The protocols used for DNA extraction and the PCR and sequencing of the Barcode fragment of the Cytochrome oxidase I (COI) gene are detailed in Puillandre et al. (2017). PCR products were purified and sequenced by the Eurofins sequencing facility. Sequences were deposited in BOLD (Barcode of Life Datasystem) and GenBank (Table 1). Newly obtained sequences were combined in a single dataset together with the sequences from Claremont et al. (2013) that corresponds to the same genera, i.e. *Cytharomorula*, *Orania* and *Tenguella* and two outgroups (*Concholepas concholepas* and *Thais nodosa*) (Table 1).

All the sequences were aligned manually (no indel was detected), and the dataset was analysed using a Bayesian approach as implemented in Mr.Bayes v. 3.2 (Huelsenbeck et al. 2001), with two runs consisting of four Markov chains of 10,000,000 generations each, with 8 chains, 5 swaps, and a sampling frequency of one tree every 2,000 generations. Each codon position of the COI gene was treated as an unlinked partition, each following a general time reversible (GTR) model, with a gamma-distributed rate variation across sites approximated in four discrete categories and a proportion of invariable sites. Convergence of each analysis was evaluated using Tracer v. 1.6 (Rambaut, Drummond, 2014) to check that all ESS values were greater than 200. The trees were then calculated after omitting the first 25% trees as burnin. Statistical support was evaluated as Bayesian posterior probability (PP).

Table 1. Species used in the phylogeny

Name	Museum ID	Expedition/locality	Station	Status	BOLD ID	GenBank ID
Cytharomorula absidata n. sp.	MNHN-IM-2007-18225	NORFOLK 2	DW2123	paratype MNHN	MUBA765-18	HE584051.1
Cytharomorula elegantula n. sp.	MNHN-IM-2013-63326	Kanacono	DW4778	holotype MNHN	MUBA780-18	MK216542
Cytharomorula grayi (Dall, 1889)	MNHN-IM-2013-66419	Walters Shoal MD 208	DW4877	MNHN	MUBA781-18	MK216540
Cytharomorula grayi (Dall, 1889)	MNHN-IM-2013-66421	Walters Shoal MD 208	DW4880	MNHN	MUBA782-18	MK216553
Cytharomorula grayi (Dall, 1889)	MNHN-IM-2013-69796	BIOMAGLO	DW4841	MNHN	MUBA779-18	MK216548
Cytharomorula grayi (Dall, 1889)	MNHN-IM-2013-69797	BIOMAGLO	DW4789	MNHN	MUBA774-18	MK216549
Cytharomorula grayi (Dall, 1889)	MNHN-IM-2013-69798	BIOMAGLO	DW4790	MNHN	MUBA778-18	MK216546
Cytharomorula grayi (Dall, 1889)	MNHN-IM-2013-69802	BIOMAGLO	DW4789	MNHN	MUBA775-18	MK216544
Cytharomorula grayi (Dall, 1889)	MNHN-IM-2013-69808	BIOMAGLO	DW4789	MNHN	MUBA776-18	MK216554
Cytharomorula grayi (Dall, 1889)	MNHN-IM-2013-69809	BIOMAGLO	DW4789	MNHN	MUBA777-18	MK216556
Cytharomorula grayi (Dall, 1889)	MNHN-IM-2013-60932	KARUBENTHOS 2015	DW4589	MNHN	MUBA772-18	MK216558
Cytharomorula grayi (Dall, 1889)	MNHN-IM-2013-61561	KARUBENTHOS 2015	DW4647	MNHN	MUBA773-18	MK216543
Cytharomorula ornamentata	MNHN-IM-2009-5587	MAINBAZA	CP3130	MNHN	MUBA770-18	HE584055.1
Cytharomorula springsteeni	MNHN-IM-2007-18184	AURORA 2007	CP2661	MNHN	MUBA767-18	HE584052.1
Cytharomorula vexillum	MNHN-IM-2007-18174	EBISCO	DW2496	MNHN	MUBA771-18	HE584062.1
Orania carnicolor (Bozzetti, 2009)	MNHN-IM-2009-14366	ATIMO VATAE	DW3608	MNHN	MUBA290-15	MK216552
Orania carnicolor (Bozzetti, 2009)	MNHN-IM-2009-22448	ATIMO VATAE	DW3608	MNHN	MUBA312-15	MK216545
Orania carnicolor (Bozzetti, 2009)	MNHN-IM-2009-22449	ATIMO VATAE	DW3608	MNHN	MUBA313-15	MK216557
Orania castanea	NHMUK 20100166	South Africa		NHMUK		HE584061.1
Orania castanea (Küster, 1858)	MNHN-IM-2013-66424	Walters Shoal MD 208	WB10	MNHN	MUBA783-18	MK216555
Orania castanea (Küster, 1858)	MNHN-IM-2013-66431	Walters Shoal MD 208	WS08	MNHN	MUBA784-18	MK216551
Orania castanea (Küster, 1858)	MNHN-IM-2013-66432	Walters Shoal MD 208	WS08	MNHN	MUBA785-18	MK216550
Orania castanea (Küster, 1858)	MNHN-IM-2013-66434	Walters Shoal MD 208	WB09	MNHN	MUBA786-18	MK216541
Orania fischeriana	MNHN-IM-2009-8832	MIRIKY	CP3288	MNHN	MUBA766-18	HE584053.1
Orania mixta	MNHN-IM-2007-18201	PANGLAO 2004	T18	MNHN	MUBA769-18	HE584054.1
Orania pacifica	MNHN-IM-2007-18193	PANGLAO 2005	DW2400	MNHN	MUBA768-18	HE584056.1
Tenguella ceylonica	NHMUK 20080822	Malaysia		NHMUK		HE584015.1
Tenguella chinoi n. sp.	NHMUK 20080772	Guam		holotype NHMUK		FN677418
Tenguella ericius n. sp.	MNHN-IM-2013-67608	Pakaihi I te Moana	MQ7-M	paratype MNHN	MUBA787-18	MK216547
Tenguella ericius n. sp.	MNHN-IM-2013-67609	Pakaihi I te Moana	MQ7-M	holotype MNHN	MUBA788-18	MK216559
Tenguella granulata	NHMUK 2007645	Seychelles		NHMUK		FN677414.1
Tenguella marginalba	NHMUK 20090088	Queensland, Australia		NHMUK		HE584016.1
Tenguella musiva	NHMUK 20080744	Malaysia		NHMUK		FN677417.1
Concholepas concholepas	NHMUK 19990303	Chile		NHMUK		EU391581
Thais nodosa	NHMUK 20070652	Ghana		NHMUK		EU391579

ABBREVIATIONS

Repository

AMS: The Australian Museum, Sydney, Australia.
HMNS: Houston Museum of Natural History, Houston, Texas, U.S.A.
IRSNB: Institut royal des Sciences naturelles de Belgique, Bruxelles, Belgium.
MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.
MHNG: Muséum d'Histoire Naturelle, Genève, Switzerland.
MNHN: Muséum national d'Histoire naturelle, Paris, France.
NHMUK: Natural History Museum, London, United Kingdom.
NMSA: The KwaZulu-Natal Museum, Pietermaritzburg, South Africa.
RH: collection of Roland Houart.

Other

IRD: Institut de Recherche pour le Développement.
WoRMS: World Register of Marine Species.

Station number prefixes

CH: Chalut de loutre (otter trawl)
DR: Drague à roches (rocks dredge)
CP: Chalut à perche (beam trawl)
DC: Drague Charcot (Charcot dredge)
DW: Drague Warén (Warén dredge)
PM: M = marées (tides)
PR: R = récoltes à vue (handpicking)

Specimens

dd: empty shell(s).
lv: live collected specimen(s)

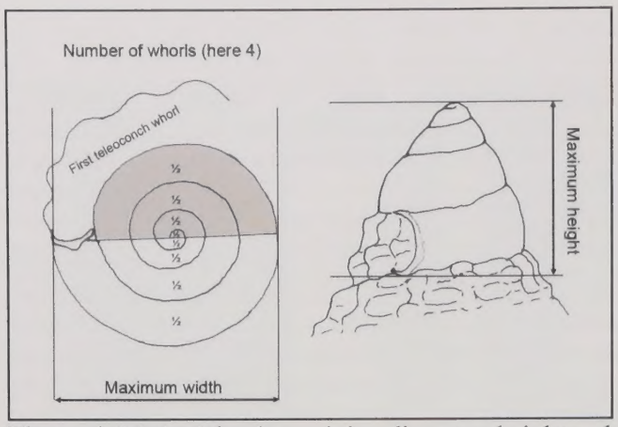


Figure 1. Method for determining diameter, height and counting the number of protoconch whorls.

Terminology used to describe the spiral cords and the apertural denticles (after Merle 2001, 2005) (Figs 10-12). Variable features are given in parentheses.

Convex part of teleoconch whorl and siphonal canal
ab: abapical (or abapertural);
abis: abapical infrasutural secondary cord on subsutural ramp;
ABP: abapertural primary cord on the siphonal canal;
ad: adapical (or adapertural);
adis: adapical infrasutural secondary cord on subsutural ramp;
ADP: adapertural primary cord on the siphonal canal;
ads: adapertural secondary cord on the siphonal canal;
IP: infrasutural primary cord on subsutural ramp;
MP: median primary cord on the siphonal canal;
ms: median secondary cord on the siphonal canal;
P: primary cord;
P1: shoulder cord;
P2-P6: primary cords of the convex part of the teleoconch whorl;
s: secondary cord;
s1-s6: secondary cords of the convex part of the teleoconch whorl (example: s1 = secondary cord between P1 and P2; s2 = secondary cord between P2 and P3, etc.);
SP: subsutural cord.
t: tertiary cord

Aperture
D1 to D5: abapical denticles;
ID: infrasutural denticle.

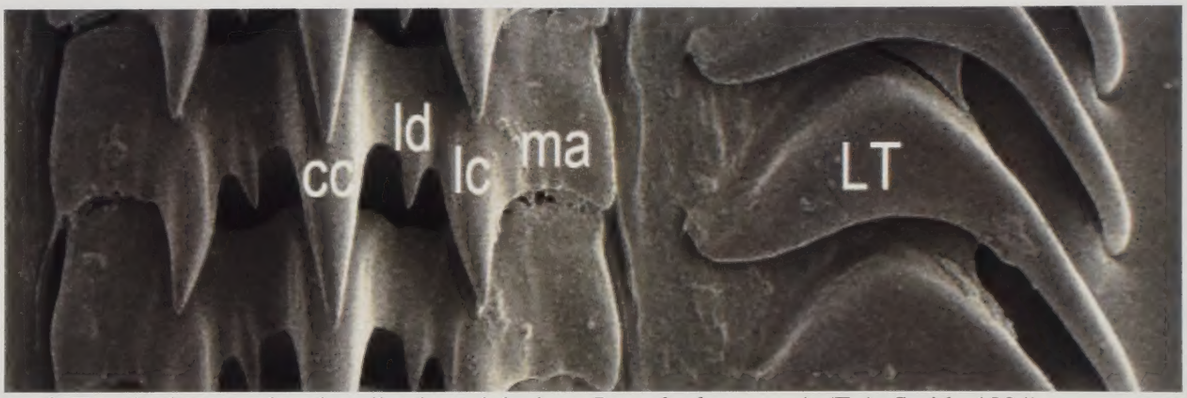


Figure 2. Terminology used to describe the radula, here *Pascula darrosensis* (E.A. Smith, 1884)
cc: central cusp; **ld:** lateral denticle; **lc:** lateral cusp; **ma:** marginal area; **LT:** lateral teeth.

Results and Discussion

Molecular analyses

In the phylogenetic tree (Fig. 3), the genera *Orania* and *Tenguella* are recovered monophyletic. *Cytharomorula* is recovered paraphyletic, contrary to the results obtained by Claremont et al. (2013), but this is probably due to the fact that we used only one gene. Each included species, and in particular, the newly described species, *Cytharomorula absidata* n. sp., *Cytharomorula elegantula* n. sp., *Tenguella chinoi* n. sp. and *Tenguella ericius* n. sp., corresponds to an independent lineage, and when several specimens per species are included, they are grouped in a single supported clade (Posterior Probabilities > 0.95).

Taxonomic implementation

Given the results obtained in Claremont et al. (2013), the phylogenetic tree presented here (Fig. 3) and the morphological analyses of additional material (see below), we propose to revise several genera of Ergalataxinae and to describe new genera and new species. The different taxa are discussed below in the order they appear in the fig. 1 of Claremont et al. (2013), following their clade naming (A, B, C, V, W, X, Y and Z); it should be noted that the clades for which we do not propose any taxonomic change or novelty are not discussed.

Purpura nodulosa C.B. Adams, 1845 has previously been assigned to *Morula* Schumacher, 1817 or *Trachypollia* Woodring, 1928 by a few authors: to *Morula* by Rios (1970, 1985), Abbott (1974), Bernard (1984) and Houart (1997); and to *Trachypollia* by Radwin & D'Attilio (1976), De Jong & Coomans (1988), Leal (1991) and Diaz Merlano & Puyana Hegedus (1994). A sister relationship between "*Morula*" *nodulosa* and all other species in major clade A was well supported in Claremont et al. (2013), who suggested to create a new genus for the western and eastern Atlantic representatives of this clade.

"Morula" nodulosa was previously included in *Morula* because its shell morphology was similar to that of species of *Tenguella*, previously considered a synonym of *Morula*. However, molecular genetic studies have shown this species to be separated from both *Tenguella* and *Morula*, as well as from *Trachypollia*. A new genus is here described to include *"Morula" nodulosa* and two other species.

Muricodrupa has long been considered to contain three species: the type species *M. fenestrata* (Blainville, 1832) (Fig. 29A-B), *M. fiscellum* (Gmelin, 1791) (Fig. 28F-H) and *M. jacobsini* Emerson & D'Attilio, 1985 (Fig. 28I). However, based on Claremont et al. (2013), *M. fiscellum* should be excluded from *Muricodrupa*, probably together with *M. jacobsini*, a different although morphologically related species. *Muricodrupa fenestrata* would then remain as the sole representative of this genus. However, Claremont et al. (2013) noted that "*Morula*" *anaxares* (Kiener, 1835) formed a marginally significant clade with *M. fenestrata*, which was not contradicted in any other analyses. Indeed, the shell morphology of "*Morula*" *anaxares* is very similar to *M. fenestrata* (Fig. 29C-D). As it is clear that "*Morula*" *anaxares* is excluded from *Morula* and *Tenguella*, we here include this species in *Muricodrupa*.

In the molecular analysis of Claremont et al. (2013), *M. fiscellum* formed a well-supported clade with "*Morula*" *rumphiusi* Houart; 1996, which was clearly excluded from *Morula* Schumacher, 1817. Both species, together with *M. jacobsini*, are morphologically distinct from the other species included in the clade B (Claremont et al. 2013), and we here assigned them to a new genus (see Table 2).

Eleven species typically assigned to *Morula* formed a monophyletic group within major clade B (subclade V) of Claremont et al. (2013). Since this subclade included *M. uva*, the type species of *Morula*, Claremont et al (2013: 27) proposed that this generic name should be restricted to this subclade. This subclade also contained *M. biconica*, the type species of *Habromorula* Houart, 1995, but the *Habromorula* species analysed by Claremont et al (2013) and assigned to this group [as a subgenus of *Morula*: *M.* (*H.*) *biconica*, *M.* (*H.*) *coronata*, *M.* (*H.*) *japonica*, *M.* (*H.*) *spinosa* and *M.* (*H.*) *striata*] did not form a clade in any analysis. However, the authors also noted that the monophyly of this morphologically distinctive group was not strongly contradicted, so further sampling and analysis could yet support *Habromorula* as a monophyletic subgenus of *Morula*.

Three species currently assigned to *Orania*, *O. gaskelli* (Melvill, 1891) (Fig. 21L), *O. serotina* (A. Adams, 1853) (Fig. 21M-N) and *O. bimucronata* (Reeve, 1846) (Fig. 21Q) formed the subclade W in the molecular phylogeny of Claremont et al. (2013), clustering with *Lataxiena fimbriata* (Hinds, 1843) (Fig. 22J) and *Usilla avenacea* (Lesson, 1842) (Fig. 21O-P), and not with the other species of *Orania* (clade Z, see below). Based on shell morphology, it is certainly possible to group *O. gaskelli*, *O. serotina* and possibly *U. avenacea* in the same genus. However, it would be difficult to justify the inclusion of *O. bimucronata* and particularly *L. fimbriata* in that morphological group, and additional studies are required before grouping them in the same genus. We suggest continuing to retain these species in the genera to which they are currently assigned: *Orania* (*O. gaskelli*, *O. serotina* and *O. bimucronata*), *Lataxiena* (*L. fimbriata*) and *Usilla* (*U. avenacea*) (see Table 2).

The type species of *Oppomorus* Iredale, 1937, *O. nodulifera* (Menke, 1829), formed a well-supported clade with *O. funiculata* (Reeve, 1846) and *O. purpureocincta* (Preston, 1909), and Claremont et al. (2013) therefore proposed that *Oppomorus* should be accorded full generic rank and not considered a subgenus of *Morula*, as had been previously proposed by Houart (2004). Three species formerly assigned to *Morula* [*M. nodulosa* (C.B. Adams, 1845), *M. parva* (Reeve, 1845) and *M. rumphiusi* Houart, 1996] were excluded from the genus.

In major clade C of Claremont et al. (2013), "*Morula*" *parva* (Reeve, 1846) was sister to all other members of subclade Z, all morphologically clearly distinct from "*Morula*" *parva*, indicating that a new genus was also required for this species.

The genus *Pascula* was also recovered as polyphyletic by Claremont et al. (2013), and is included in their Clade C, subclade Z, together with *Cytharomorula* and *Orania*. The type species of *Pascula*, *P. citrica* (Dall, 1908) (Fig. 22K-L) was not analysed in that study. However, the study did include a related species, *P. darrosensis* (E.A. Smith, 1884), with a similar radula morphology (Figs 7F and 22M-N). Pending further genetic research all species previously included in *Pascula* are here retained in this genus (see Table 2).

Based on the results of the present analysis, and also because the shell morphology of the type species of *Orania* [(*Orania fusulus* (Brocchi, 1814)], as well as that of other *Orania* species, is similar to the shell morphology of *Cytharomorula*, the latter could be considered a possible junior synonym of *Orania*, pending future research. Indeed, Claremont et al. (2013: subclade Z) considered the validity of *Cytharomorula* uncertain, as this genus was not monophyletic in any analysis. However, this non-monophyly was due to the presence of *Orania ornamentata* Houart, 1995 (Fig. 13D-E) in the *Cytharomorula* clade. The shell morphology of *O. ornamentata* is strongly similar to that of the type species of *Cytharomorula* (*C. vexillum* Kuroda, 1953) (Fig. 13A-C), and we thus re-assign *O. ornamentata* in *Cytharomorula*. This renders the *Cytharomorula* of Claremont et al. (2013: subclade Z) monophyletic. Unfortunately, as long as *Orania fusulus* (Brocchi, 1814) (Fig. 21A-C), the type species of *Orania*, has not been analysed genetically, it will remain unclear whether *Cytharomorula* should be considered a junior

synonym of *Orania* or not. Here, we still consider that *Orania* and *Cytharomorula* are two distinct genera.

Four ergalataxine genera were not included in Claremont et al. (2013) because of a lack of appropriate material, and the type species were not analysed for two additional genera (Table 2). The inclusion of these four genera in the Ergalataxinae, and the composition of *Orania* and *Pascula,* therefore remains doubtful. Their classification is primarily based on morphological shell and/or radula characters.

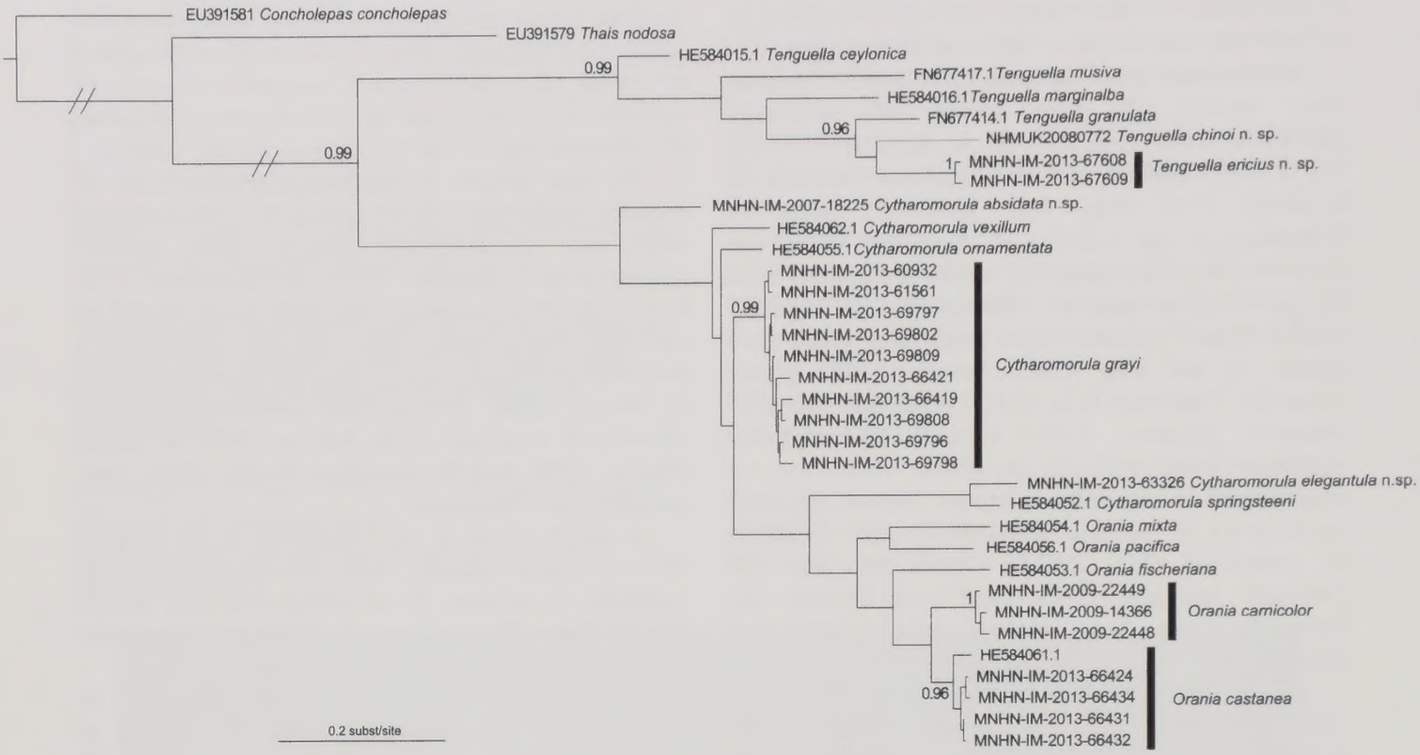


Figure 3. Bayesian phylogeny of Ergalataxinae included in this paper and rapanine outgroups

SYSTEMATIC ACCOUNT

Family **MURICIDAE** Rafinesque, 1815
Subfamily **ERGALATAXINAE** Kuroda, Habe & Oyama, 1971
Genus ***Cytharomorula*** Kuroda, 1953
Type species by monotypy: *Cytharomorula vexillum* Kuroda, 1953, Japan (Fig. 13A-C)

Diagnosis. Shell with high spire, elongate, ovate or broadly ovate, weakly nodose, not or rarely exceeding 20 mm in length at maturity. Axial sculpture of last teleoconch whorl consisting of 8 or 9 narrow, high, rounded ribs. Spiral sculpture of low or moderately high, narrow, rounded, low, primary and secondary cords and few threads.
Aperture ovate. Columellar lip weakly concave, smooth or with weak, narrow knobs abapically, rim almost entirely adherent to shell. Anal notch broad, deep. Outer lip with narrow, obvious denticles within. Siphonal canal short, broadly open ventrally.
Radula of the type species (Fig. 6A) with three dimensional rachidian tooth bearing a long, narrow, projecting central cusp, a small, very narrow lateral denticle, a moderately long, narrow, lateral cusp and weak marginal folds. No marginal cusp. Lateral teeth sickle shaped, with broad base.

Remarks. The genus *Cytharomorula* includes 10 Recent species in WoRMS (MolluscaBase 2018): *Cytharomorula ambonensis* (Houart, 1996) (Indo-West Pacific); *C. benedicta* (Melvill & Standen, 1895) (Pacific Ocean); *C. danigoi* Houart, 1995 (Pacific Ocean); *C. dollfusi* (Lamy, 1938) (Indo-West Pacific); *C. grayi* (Dall, 1889) (western and eastern Atlantic, southwestern Indian Ocean); *C. lefevreiana* (Tapparone Canefri, 1880) (western Indian Ocean); *C. paucimaculata* (Sowerby, 1903) (Japan); *C. pinguis* Houart, 1995 (New Caledonia, New Hebrides Arc and Tonga); *C. springsteeni* Houart, 1995 (Indo-West Pacific); *C. vexillum* Kuroda, 1953 (Pacific Ocean). Only one of these species occurs in the Atlantic, all others are found in the Indo-West Pacific region. A revision of a few species (*Cytharomorula ambonensis*, *C. benedicta*, C. *dollfusi*, *C. lefevreiana* and *C. paucimaculata*) was recently published (Houart, 2013a). Five additional new species from the Indo-West Pacific are described below, and a new combination is given for *C. ornamentata* (Houart, 1995), which gives us a total of 16 species for this genus.

In several species the primary spiral cord P4 is generally broader and larger, with broader, more conspicuous knobs at the intersection with the axial ribs.

Cytharomorula absidata n. sp.
Figs 4; 11F; 13F-L

Type material. Holotype MNHN-IM-2000-34201, New Caledonia, NORFOLK 2, stn DW2123, 23°18'S, 168°15'E, 187-197 m.
Paratypes: New Caledonia, NORFOLK 2, stn DW2123, 23°18'S, 168°15'E, 187-197 m, 1 lv, paratype MNHN-IM-2007-18225 (BOLD MUBA765-18; GenBank HE584051.1); SMIB 5, stn DW93, 22°20'S, 168°43'E, 240-255 m, 1 dd, MNHN-IM-2010-23374.

Type locality. New Caledonia, 23°18'S, 168°15'E, 187-197 m.

Distribution. Southern New Caledonia, living at 187-197 m.

Description. Shell medium sized for the genus, up to 13 mm in length at maturity (paratype MNHN). Length/width ratio 2.0 (paratype). Lanceolate, biconical, broadly ovate. Subsutural ramp broad, strongly sloping, concave.
Shell creamy white, axial ribs light orange coloured near suture. Light tan on crest of some primary spiral cords and at tip of siphonal canal. Aperture white.
Spire high, acute, with 3+ protoconch whorls (tip broken). Teleoconch up to 5 broad, strongly convex, weakly shouldered whorls. Suture strongly adpressed. Protoconch moderately small, conical, acute. Whorls smooth, glossy. Maximum width 850 µm. Terminal lip of sinusigera type.
Axial sculpture consisting of high, broad, rounded, weakly nodose ribs. Ribs of last whorl connected to preceding whorl with strong buttresses. Other axial sculpture consisting of numerous, very narrow, small, growth lamellae. Spiral sculpture of low, rounded, narrow, smooth primary, secondary and tertiary cords, and additional, few smooth threads. Primary and secondary cords of same strength, tertiary cords narrow. Last whorl with SP, adis, IP, abis, P1, s1, P2, s2, P3, s3, P4, s4, P5, s5, P6, s6, ADP, (ads), MP, ms, ABP, (abs).
Aperture moderately small, ovate. Columellar lip narrow, smooth except 2 or 3 weak knobs abapically. Rim adherent, weakly erect on a small portion abapically. Anal notch deep, broad. Outer lip smooth, with low, narrow denticles within: ID, D1 and D2 fused, D3, D4 and D5. Siphonal canal short, narrow, straight, narrowly open.
Operculum and radula unknown.

Remarks. This is the species identified as *Cytharomorula* cf. *grayi* from New Caledonia (MNHN-IM-2007-18225) and analyzed in Claremont et al. (2013).
Cytharomorula elegantula n. sp. differs from *C. absidata* n. sp. in having a higher, more elongate spire, less shouldered teleoconch whorls, a less concave subsutural ramp and a relatively narrower last teleoconch whorl. The spiral cord morphology differs also, consisting of narrower primary, secondary and tertiary cords and more widely spaced primary cords in *C. elegantula* n . sp.
Cytharomorula pinguis Houart, 1995 (Fig. 18M-N) differs greatly from *C. absidata* n. sp. in having a higher spire, strong columellar folds and heavy outer apertural lip denticles, a broader outer apertural lip and much broader, flat, spiral cords.
Cytharomorula springsteeni (Figs 10F; 13M-O) also recorded in New Caledonia differs in its shell morphology. *C. springsteeni* has also a strongly concave subsutural ramp and adpressed suture, but the shell is lighter, more fragile, with a slightly narrower last teleoconch whorl, narrower axial ribs, less expanded on the preceding whorl, and narrower spiral cords.
Cytharomorula manusuduirauti n. sp. a species here described from the Philippines (Fig. 18G-L), is a smaller shell, also with broad axial ribs but which are obviously less expanded on the penultimate whorl. The numerous, narrower, primary, secondary and tertiary cords are of approximately similar strength in *C. manusuduirauti* and more crowded than in *C. absidata* n. sp.

Etymology. *absidatus* (*a*) (L): arched, named for the strongly arched form of the last teleoconch whorl.

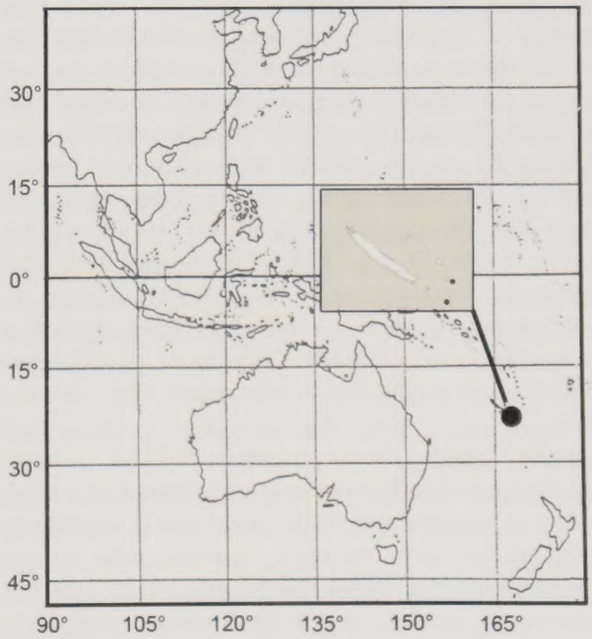


Figure 4. Distribution of *Cytharomorula absidata* n. sp.

Cytharomorula arta n. sp.
Figs 5; 10A-B; 15A-E

Type material. Holotype MNHN-IM-2000-34203, Reunion, MD32 (REUNION), stn CP57, 21°05'S, 55°11'E, 210-227 m, dd.
Paratypes: Reunion, MD32, stn DC2, 21°12'S, 55°49'E, 160-190 m, 2 dd, MNHN-IM-2000-34204; stn DC56, 21°05'S, 55°12'E, 1982, 170-225 m, 7 dd, MNHN-IM-2000-34205; stn CP57, 21°05'S, 55°11'E, 210-227 m, dd, 1 MNHN-IM-2000-34206; stn DC176, 21°02'S, 55°11'E, 165-195 m, 1 dd, MNHN-IM-2000-34207, 1 dd, RH.

Type locality. Western Indian Ocean, Reunion, 21°05'S, 55°11'E, 210-227 m.

Distribution. Western Indian Ocean, East Reunion Island, 190-210 m (dd) (Fig. 5).

Description. Shell small for the genus, up to 14.3 mm in length at maturity (holotype). Length/width ratio 2.0-2.2. Slender, lanceolate, narrow, nodose, lightly built. Subsutural ramp broad, strongly sloping, weakly concave.
Creamy-white or light tan with numerous spiral cords topped with brown. Tip of siphonal canal light brown. Aperture white.
Spire very high, acute, with 3.5-4 protoconch whorls and teleoconch up to 5 weakly convex, elongate, weakly angulate, weakly shouldered, nodose whorls. Suture of whorls adpressed. Protoconch small, conical, whorls smooth, glossy, height and width 900 µm. Terminal lip of sinusigera type.
Axial sculpture of teleoconch whorls consisting of moderately high, broad, nodose ribs. First whorl with 9 ribs, second with 9 or 10, third with 10 or 11, fourth with 10-12, last whorl with 8 or 9 ribs. Occasional presence of a single varix on penultimate and last whorls. Spiral sculpture of high, rounded, nodose, primary, secondary and tertiary cords. First whorl with visible IP, P1 and P2 or P1-P3; second with SP, adis, IP, abis, P1, s1, P2, s2, P3 with additional tertiary cords on third and fourth whorls. Last teleoconch whorl with SP, adis, IP, abis, SP, P1, s1, P2, s2, P3, s3, P4, s4, P5, s5, P6, ADP, MP, ms and ABP with additional tertiary cords (Fig. 10A). Cords of approximately similar size except broader and higher P4, usually lighter coloured. Crossing of axial ribs and primary cords giving rise to low nodes, more obvious on P4.
Aperture narrow, ovate. Columellar lip narrow, smooth, rim partially weakly erect, adherent at a small portion at adapical extremity. Anal notch moderately deep, broad. Outer lip erect, smooth, with 6 low, elongate denticles within, consisting of IP, D1-D5, occasionally obsolete (Fig. 10B). Siphonal canal short, 17% of total shell length in holotype, narrow, weakly dorsally recurved, broadly open.
Operculum and radula unknown.

Remarks. *Cytharomorula springsteeni* (Figs 10F; 13M-O), a species currently known from several localities in the Pacific Ocean (New Caledonia, Vanuatu, Philippines and the Marquesas), differs from *C. arta* n. sp. in having a comparatively broader shell with a slightly steeper shoulder ramp, more shouldered teleoconch whorls, a shorter, less elongate spire, and a weakly narrower, longer siphonal canal.
Cytharomorula elegantula n. sp. described herein (Figs 10C; 16H-N) differs in having a comparatively larger and broader shell reaching 17.3 mm in length, a broader anal notch, a small but obvious parietal tooth and a low, narrow, weak, elongate knob on the adapical part of the columellar lip, which is smooth in *C. arta* n. sp. Young specimens of *C. arta* n. sp. and *C. elegantula* n. sp. are oddly similar (Fig. 10 A & C), but *C. elegantula* still differs in having a broader, larger shell for a same number of teleoconch whorls, a low, broad SP, a comparatively narrower siphonal canal and already in young specimens a very low parietal tooth and a low knob on the columellar lip.
Cytharomorula lefevreiana (Fig. 15F-G), another species occurring off Mauritius and Reunion that was collected during the MD32 cruise (Houart, 2013a), differs in many aspects, including having a comparatively smaller and narrower shell, from 7 to 11 mm in length, more strongly shouldered whorls with very obvious P1-P3 spiral cords, and a relatively smaller aperture.

Etymology. *Arta* (L): meaning narrow, named for its narrow shell.

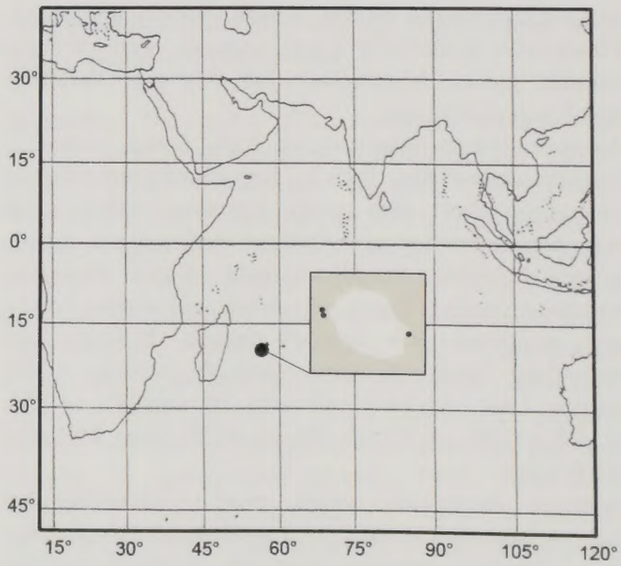


Figure 5. Distribution of *Cytharomorula arta* n. sp.

CYTHAROMORULA GRAYI GROUP

A very careful comparative study of shell and genetic characters, including additional newly available material, indicates that specimens identified or doubtfully identified as *C. grayi* (Dall, 1889),

distributed in five distinct areas, represent in fact three distinct species. *C. grayi* s.s. lives in the tropical western and eastern Atlantic with a range extension which includes south-eastern South Africa and the south-western Indian Ocean; a second species, *C. elegantula* n. sp., is limited to the southwest Pacific, in New Caledonia, Vanuatu and Tonga; and a third, *C. fatuhivaensis* n. sp., is restricted to the Marquesas Archipelago. In the present state of our knowledge, none of these species appear to have overlapping ranges.

Cytharomorula grayi (Dall, 1889)
Figs 10D; 11A-B; 14; 15H-P

Nassaria (*Nassarina*) *grayi* Dall, 1889: 183, pl. 32, fig. 12a.
Cantharus (*Tritonidea*) *laevis* E.A. Smith, 1890: 261, pl. 21, fig. 11.
Trophon lowei Watson, 1897: 244, pl. 19, fig. 12.
Cytharomorula (?) *grayi* — Houart, Kilburn & Marais, 2010: 223.

Not *Cytharomorula grayi* — Houart, 1995: 254, figs 9-10, 67-68; Houart & Héros, 2008: 459 (= *C. elegantula* n. sp.)
Not *Cytharomorula* sp. cf. *C. grayi* — Tröndlé & Houart, 1992: 88, fig. 48 (= *C. fatuhivaensis* n. sp.).
Not *Cytharomorula grayi* — Houart & Tröndlé, 2008: 70, 92 (= *C. fatuhivaensis* n. sp.).
Not *Cytharomorula grayi* — Tsuchiya, 2000: 381, pl. 189, fig. 87; Tsuchiya, 2017: 954, pl. 247, fig. 3 (= *Cytharomorula* sp.).

Type material. *Nassaria* (*Nassarina*) *grayi* Dall, 1889: The specimen illustrated by Dall (MCZ 7256) was "removed" from its box in the MCZ, and the specimen presently in the box labelled *C. grayi* is not *C. grayi* but another species, not even a muricid (Houart & Tröndlé, 1992; Vokes, 1996), but rather a buccinid. Nevertheless, the original figure in Dall (1889: pl. 32, fig. 12a) is excellent and its identity is undoubtable. The specimen illustrated by Dall was designated as the lectotype by Vokes (1996: 29); *Cantharus* (*Tritonidea*) *laevis* E.A. Smith, 1890: lectotype NHMUK 1889.10.1.2362 (Fig. 15O-P), designated by Vokes (1996: 29) (see remarks) and 4 paralectotypes NHMUK 1889.10.1.2363-2366; *Trophon lowei* Watson, 1897: lectotype NHMUK 1911.7.17.2 (Fig. 15N), designated by Houart & Abreu (1994: 122) (see remarks).

Type localities. *Nassaria* (*Nassarina*) *grayi* Dall, 1889: off Barbados, in 73 fathoms (133.5 m), *Blake* Station 290; *Cantharus* (*Tritonidea*) *laevis* E.A. Smith, 1890: Saint Helena; *Trophon lowei* Watson, 1897: Madeira.

Other material examined. Western Atlantic: East of Guadeloupe (south of Désirade), 250 m, 2 lv, RH; west coast of Barbados, 165 m, 1 lv, RH; southeastern Brazil, MD55 (BRESIL), stn DC55, 20°32'S, 28°52'W, 780-795m, 12 dd, MNHN-IM-2012-33133; MD55, stn CB103, 23°36'S, 42°02'W, 200-217 m, 1 lv, MNHN-IM-2012-33127.
Eastern Atlantic: Canary Islands, Gran Canaria, Sardina, dredged, 2 lv, RH; Canary Islands, Tenerife, Palma, 150-200 m, 52 lv, RH; Madeira, Porto Santo, 1 lv, RH; Madeira, Funchal Bay, 100 m, 1 lv, RH; Madeira (no other data), 1 lv, RH.
South Africa: Durban, off Umlaas Canal, 128 m, 1 lv, NM B6282; South Africa, Transkei, off Mtamvuna River, 31°08'S, 30°17'E, 160 m, 1 dd, NM C9646; southern Natal, 75-95m, in grit samples, 3 lv, coll. Roy Aiken; 1 dd, RH.
Walters Shoal: MD208, stn DW4877, 33°10'S, 43°49'E, 217-256 m, 1 lv, MNHN-IM-2013-66418, 1 lv, MNHN-IM-2013-66419 (BOLD MUBA781-18; GenBank MK216540); stn DW4880, 33°17'S, 43°51'E, 275-318 m, 2 lv, MNHN-IM-2013-66421 (BOLD MUBA782-18; GenBank MK216553); stn DW4885, 33°17'S, 43°55'E, 272-380 m, 2 lv, 1 MNHN, 1 RH; stn DW4894, 33°09'S, 43°50'E, 199-261 m, 2 lv, MNHN; stn DW4896, 33°07'S, 43°51'E, 325-357 m, 1 dd, MNHN; stn DW4897, 33°09'S, 43°59'E, 490-584 m, 1 lv, MNHN.
Mozambique Channel: MAINBAZA, stn DW3167, Almirante Leite Bank, 26°12'S, 35°02'E, 228-230 m, 3 dd, MNHN.
Reunion: MD32 (REUNION), stn DC2, 21°12'S, 55°49'E, 160-190 m, 3 dd, MNHN; stn DC128, 20°51'S, 55°36'E, 280-340 m, 1 dd, MNHN; stn CP129, 20°51'S, 55°36'E, 290-300 m, 1 dd, MNHN.
Mayotte, Comoros and Glorieuses Islands: BIOMAGLO, stn DW4789, 12°22'S, 46°25'E, 340-342 m, 4 lv, MNHN-IM-2013-69797 (BOLD MUBA774-18; GenBank MK216549), MNHN-IM-2013-69802, (BOLD MUBA775-18; GenBank MK216544), MNHN-IM-2013-69808, (BOLD MUBA776-18; GenBank MK216554), MNHN-IM-2013-69809, (BOLD MUBA777-18; GenBank MK216556); stn DW4790, 12°22'S, 46°25'E, 360-375 m, 1 lv, MNHN-IM-2013-69798 (BOLD MUBA778-18; GenBank MK216546); stn DW4841, 12°23'S, 43°33'E, 154-333m, 1lv, MNHN-IM-2013-69796 (BOLD MUBA779-18; GenBank MK216548).
Glorieuses Islands: SW Grande Glorieuse, BENTHEDI, stn 93DS, 11°32'S, 47°16'E, 480-550 m, 1 dd, MNHN.

Distribution. *Cytharomorula grayi* occurs from the Lesser Antilles in 100-450 m (Garrigues & Lamy 2018) to southern Brazil in the western Atlantic, and in the eastern Atlantic in the Canary Islands, Madeira and the banks off Portugal, but not on the mainland European continental shelf (SEAMOUNT 1 cruise material in MNHN). The species also occurs off Saint Helena and extends its range to South Africa, Walters Shoal, Mozambique, Reunion, Mayotte, Comoros and

Glorieuses Islands, Indian Ocean, there living in 128-275 m (Fig. 14).

Remarks. Vokes (1996: 29) mentioned and illustrated the originally figured syntype of *Cantharus laevis* as the holotype. Smith (1890) never designated any shell as the holotype. The type material in the NHMUK consists of 5 specimens, mentioned as syntypes by Houart (1997: 56). Vokes (1996) only mentions what she then called the "holotype", but having examined the material when visiting the NHMUK she certainly was aware of the existence of the other 4 specimens. The mention of Vokes is here considered as an indirect lectotype designation by inference as holotype, following ICZN Art. 74.5: "*In a lectotype designation made before 2000, either the term "lectotype", or an exact translation or equivalent expression (e.g. "the type"), must have been used or the author must have unambiguously selected a particular syntype to act as the unique name-bearing type of the taxon. When the original work reveals that the taxon had been based on more than one specimen, a subsequent use of the term "holotype" does not constitute a valid lectotype designation unless the author, when wrongly using that term, explicitly indicated that he or she was selecting from the type series that particular specimen to serve as the name-bearing type*".
Houart & Abreu (1994: 122, fig. 5) illustrated the syntype and only existing specimen of *Trophon lowei* as the holotype. This is here also considered as a valid lectotype designation following ICZN Art. 74.6: "*When it has been accepted that a nominal species-group taxon was based on a single specimen and the original description neither implies nor requires that there were syntypes, and if it is considered subsequently that the original description was based on more than one specimen, the first author to have published before 2000 the assumption that the species-group taxon was based upon a single type specimen is deemed to have designated that specimen as the lectotype*".

Discussion. Material consisting of numerous live and dead collected specimens from the southwestern Indian Ocean was examined and initially considered a separate species. Adult specimens are bigger than the typical Atlantic *Cytharomorula*, wider and more shouldered, have a slightly wider aperture and a narrower siphonal canal (Figs 11A-B; 16A-G). Nevertheless, genetic analysis performed on specimens from Guadeloupe (KARUBENTHOS 2), Walters Shoal (MD 208) and other specimens collected off Mayotte, Comoros and Glorieuses islands confirm the conspecifity of the populations of the Atlantic Ocean and the Indian Ocean. The type material of *Trophon lowei* (Madeira) (Fig. 15N) and *Cantharus laevis* (Saint Helena) (Fig. 15O-P) seems to be composed of intermediate forms between the populations of the western Atlantic and the Canary Islands (Fig. 15H-L) and those of the Indian Ocean.

Cytharomorula elegantula n. sp.
Figs 6B-C; 10C; 14; 16H-N

Cytharomorula grayi — Houart, 1995: 254, figs 9-10, 67-68; Houart & Héros, 2008: 459 [(not *C. grayi* (Dall, 1889)].

Type material. Holotype MNHN-IM-2013-63326 (BOLD MUBA780-18; GenBank MK216542), New Caledonia, KANACONO, stn DW4778, 23°03'S, 168°18'E, 170-248 m.
Paratypes: **New Caledonia,** KANACONO, stn DW4741, 22°52'S, 167°41'E, 210-210 m, 1 lv, MNHN-IM-2013-63337;
KANADEEP, stn DW4945, 25°22'S, 159°43'E, 108-130 m, 1 lv, MNHN-IM-2013-48638;
BIOCAL, stn DW66, 24°55'S, 168°22'E, 505-515 m, 2 lv, MNHN-IM-2010-23359 (radula illustrated in Houart, 1995: figs 9-10 and reproduced here Fig. 6B-C);
SMIB 4, stn DW46, 24°47'S, 168°09'E, 260 m, 1 lv, MNHN-IM-2010-23369;
SMIB 8, stn DW154, 24°46'S, 168°08'E, 235-252 m, 13 lv & dd, 11 MNHN-IM-2000-34208, 2 RH; stn DW159, 24°46'S, 168°08'E, 241-245 m, 9 lv & dd, MNHN-IM-2000-34209; stn DW167, 23°38'S, 168°43'E, 430-452 m, 2 lv, MNHN-IM-2010-23357.

Type locality. South of New Caledonia, 24°48'S, 168°09'E, living at 245 m.

Other material examined. New Caledonia. BIOCAL: stn DW65, 24°48'S, 168°10'E, 245-275 m, 1 dd, MNHN-IM-2010-23360;
CHALCAL 2: stn CH8, 23°13'S, 168°03'E, 300 m, 3 dd, MNHN-IM-2010-23366; stn DW69, 24°44'E, 168°08'E, 260 m, 1 dd, MNHN-IM-2010-23365; stn DW70, 24°46'S, 168°09'E, 232 m, 1 lv, MNHN-IM-2010-23364; stn DW71, 24°42'S, 168°10'E, 230 m, 8 lv & dd, MNHN-IM-2010-23363;
SMIB 3: stn DW8, 24°45'S, 168°08'E, 233 m, 2 dd, MNHN-IM-2010-23368; DW14, 23°40'S, 167°60'E, 246 m, 4 lv & dd, MNHN-IM-2010-23367;
SMIB 4: stn DW44, 24°46'S, 168°08'E, 300 m, 1 dd, MNHN-IM-2010-23371; stn DW49, 24°46'S, 168°09'E, 300 m, 1 dd, MNHN-IM-2010-23370;
SMIB 5: stn DW95, 22°60'S, 168°20'E, 200 m, 1 dd, MNHN-IM-2010-23372; stn DW96, 23°00'S, 168°19'E, 245 m, 1 dd, MNHN-IM-2010-23373;
SMIB 8: stn DW159, 24°46'S, 168°08'E, 241-245 m, 1 lv, MNHN-IM-2010-23356;
BERYX 11: stn DW11+CP23, 24°44'S, 168°10'E, 320-350 m, 1 dd, MNHN-IM-2010-23361; DW18, 24°48'S, 168°09'E, 250-270 m, 3 dd, MNHN-IM-

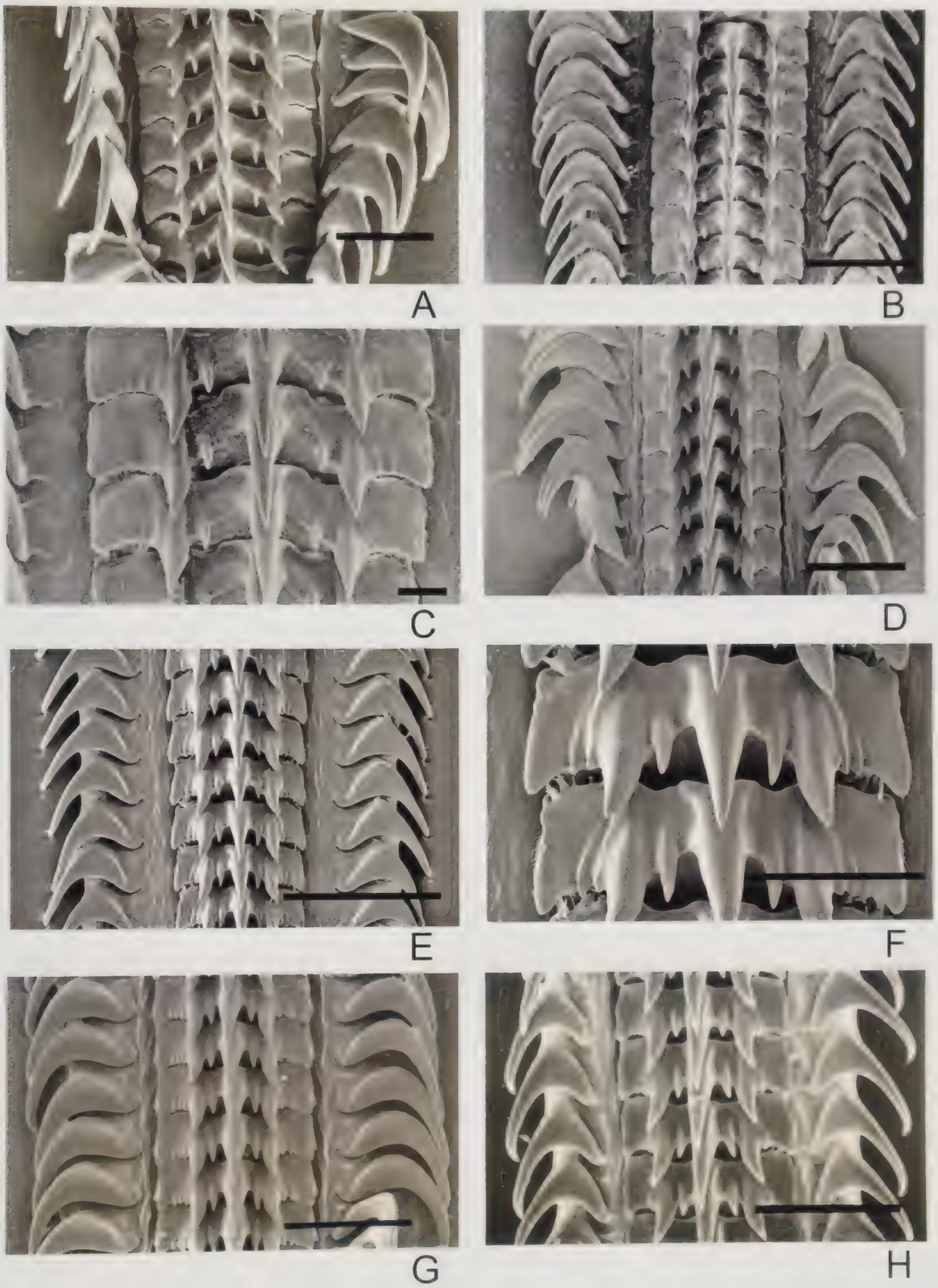


Figure 6 – Radulae
A. *Cytharomorula vexillum* Kuroda, 1953, New Caledonia. Scale bar: 50 µm (SEM A. Warén)
B-C. *Cytharomorula elegantula* n. sp., New Caledonia. Scale bars: B. 100 µm; C. 20 µm (SEM P. Bouchet)
D. *Cytharomorula ornamentata* (Houart, 1995), Transkei, Sourth Africa. Scale bar: 50 µm (SEM A. Warén)
E-F. *Orania carnicolor* Bozzetti, 2009, Madagascar. Scale bars: E: 50 µm; F. 20 µm (SEM A. Warén)
G. *Orania fusulus* (Brocchi, 1814), Angola. Scale bar: 50 µm (SEM A. Warén)
H. *Orania castanea* (Küster, 1858), East London, South Africa. Scale bar: 50 µm (SEM A. Warén)

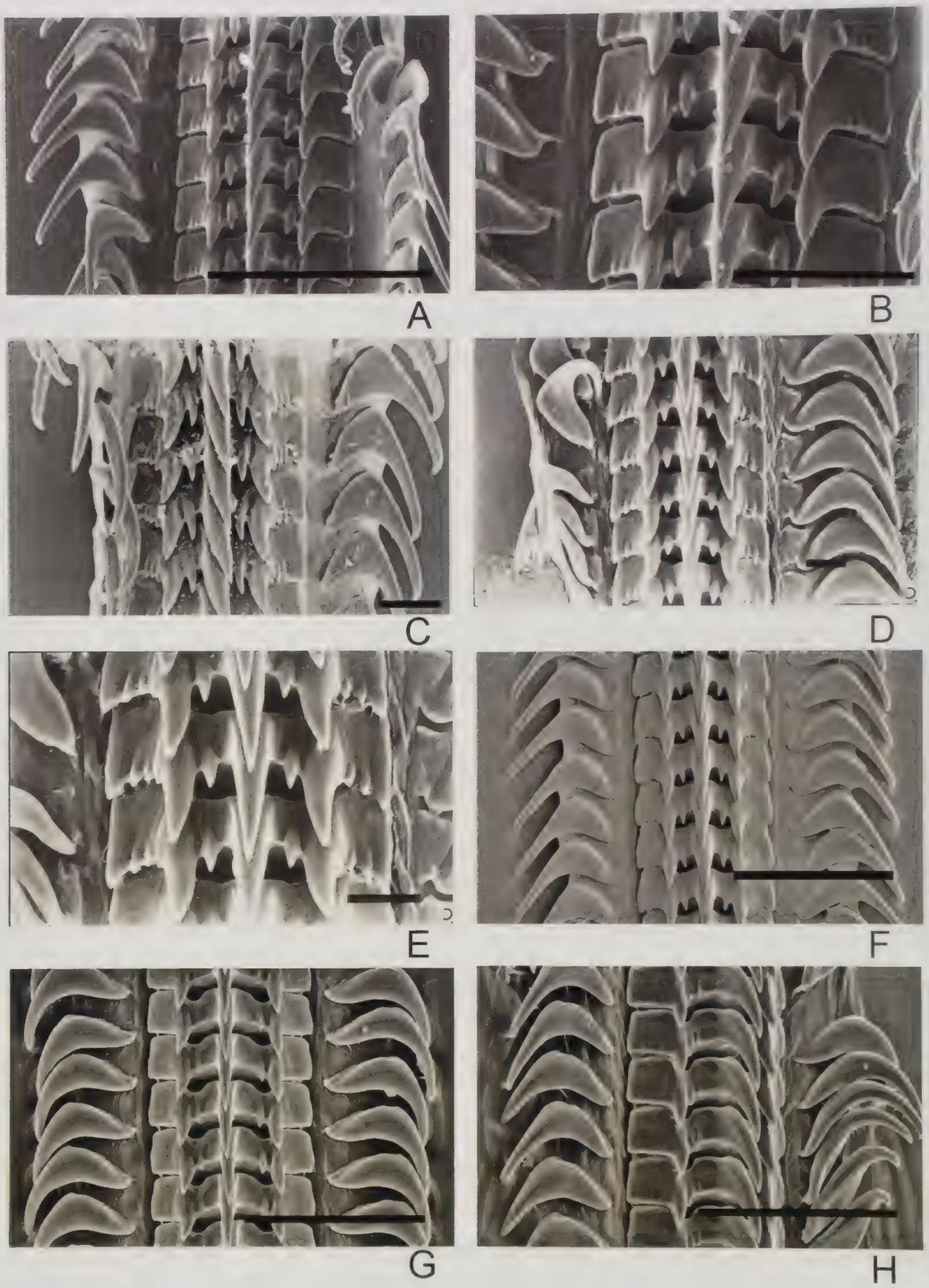


Figure 7 – Radulae
A-B. *Orania pseudopacifica* n. sp. Marquesas, MUSORSTOM 9, stn CP1239, paratype MNHN-IM-2000-34213. Scale bar: A. 100 µm, B. 50 µm (SEM Y. Kantor).
C. *Orania pacifica* (Nakayama, 1988), Philippines. Scale bar: 20 µm (SEM P. Bouchet)
D-E. *Orania pleurotomoides* (Reeve, 1845), Papua New Guinea. Scale bar 10 µm (SEM P. Bouchet)
F. *Pascula darrosensis* (E.A. Smith, 1884), Philippines. Scale bar: 50 µm (SEM A. Warén)
G-H. *Pascula palmeri* (Powell, 1967), New Zealand, W of Maroro Point, Aorangi Island, Poor Knights Islands. 35°28.57 S – 174°44.18 E, 5-20 m. NMNZ M.164595. Scale bar: 200 µm (SEM Y. Kantor)

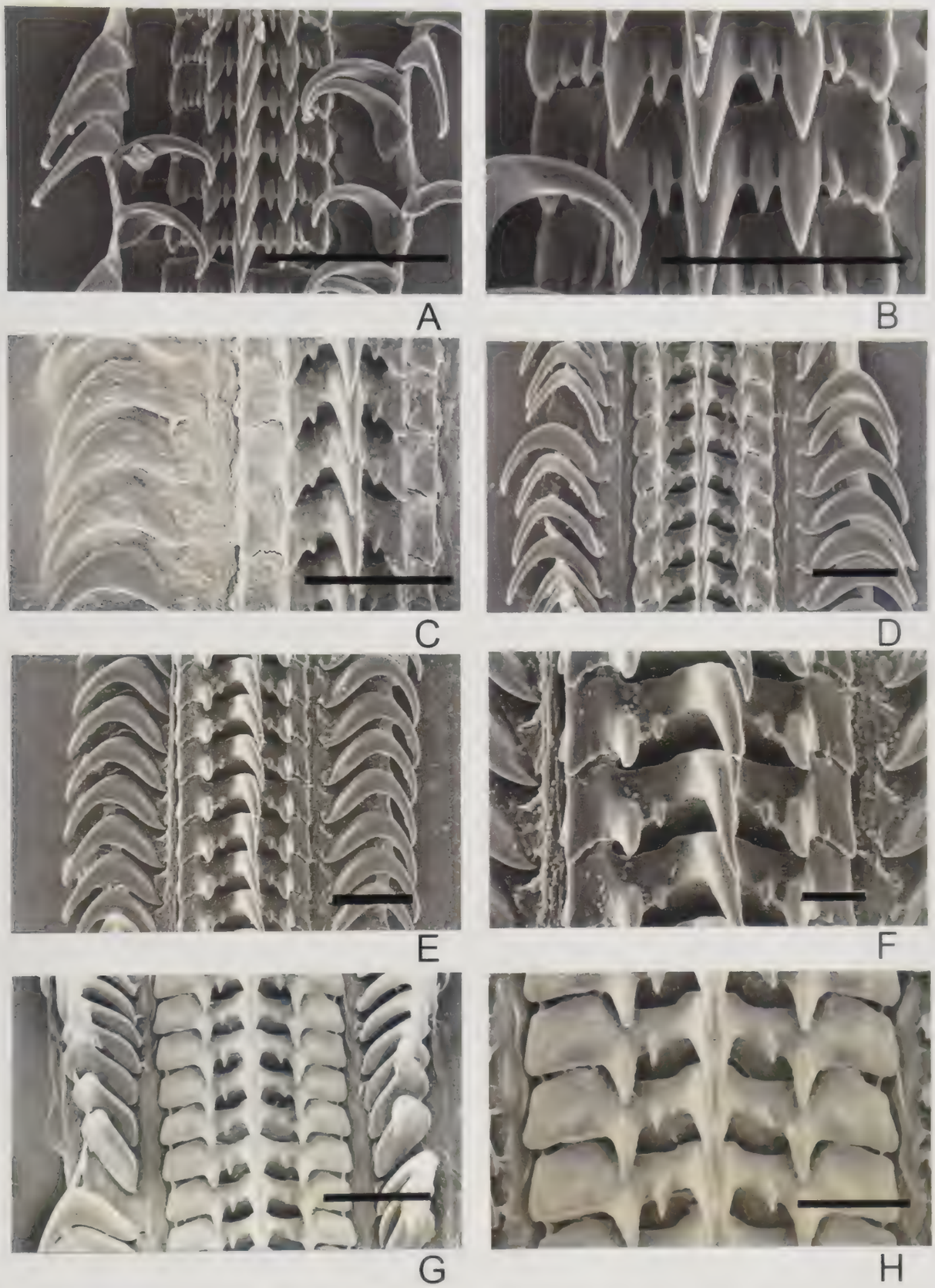


Figure 8 – Radulae
A-B. *Tenguella chinoi* n. sp., Vanuatu, SANTO, stn RAP15, paratype MNHN-IM-2000-34215. Scale bar: A. 50 µm, B. 30 µm (SEM Y. Kantor)
C. *Tenguella granulata* (Duclos, 1832), Gulf of Aden. Scale bar: 50 µm (SEM A. Warén)
D. *Claremontiella adiakritos* n. sp., San Felipe, Baja California. Scale bar: 50 µm (SEM A. Warén)
E-F. *Claremontiella consanguinea* (E.A. Smith, 1891), São Tomé. Scale bar: G: 50 µm, H: 20 µm (SEM P. Bouchet)
G-H. *Murichorda rumphiusi* (Houart, 1995), Ambon. Scale bars: C: 100 µm; D: 50 µm (SEM A. Warén)

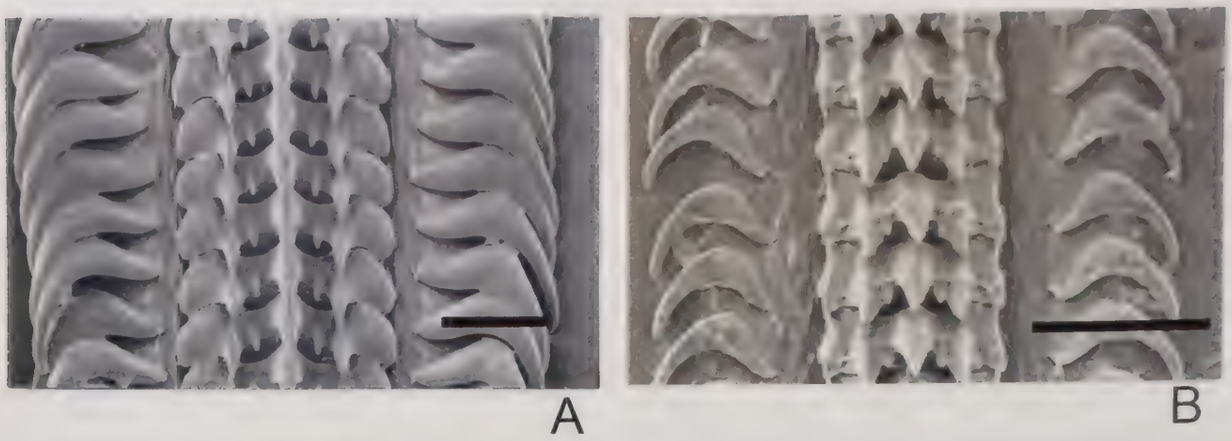


Figure 9 – Radulae

A. *Murichorda fiscellum* (Gmelin, 1791), Ambon. Scale bar: 50 µm (SEM A. Warén)
B. *Muricodrupa anaxares* (Kiener, 1835), Ambon. Scale bar: 50 µm (SEM A. Warén)

2010-23362; stn CP25, 24°44'S, 168°09'E, 230-235 m, 1 lv;
BATHUS 2: stn DW739, 22°35'S, 166°27'E, 465-525 m, 1 dd;
LIFOU 2000: stn 1462, 20°47'S, 167°03'E, 70-120 m, 1 dd, MNHN-IM-2010-21108;
NORFOLK 1: stn 1674, 23°40'S, 168°00'E, 245-253 m, 2 dd, MNHN-IM-2010-23354; stn DW1675, 24°45'S, 168°09'E, 231-233 m, 9 dd, MNHN-IM-2010-23350; stn CP1677, 24°44'S, 168°09'E, 233-259 m, 1 lv, MNHN-IM-2010-23352; stn DW1724, 23°17'S, 168°14'E, 200-291 m, 1 dd, MNHN-IM-2010-23351; stn DW1726, 23°18'S, 168°15'E, 185-207 m, 2 dd, MNHN-IM-2010-23353; stn DW1727, 23°17'S, 168°14'E, 190-212 m, 4 dd, MNHN-IM-2010-23349;
NORFOLK 2: stn DC2089, 24°44'S, 168°09'E, 227-230 m, 3 dd; stn DW2093, 24°44'S, 168°09'E, 230 m, 1 lv (MNHN-IM-2007-18205), 5 dd;
EBISCO: stn DW2639, 20°47'S, 161°01'E, 289-294 m, 1 dd, MNHN-IM-2010-5135;
TERRASSES: stn DW3103, 23°02'S, 168°21'E, 180-220 m, 2 dd;
EXBODI: stn DW3866, 22°52' S, 169°26' E, 100 m, 1 lv, MNHN-IM-2009-22839; stn DW3867, 22°52'S, 169°26'E, 146-610 m, 1 dd, MNHN-IM-2014-2394;
KANACONO: stn DW4763, 23°17'S, 168°15'E, 192-260 m, 3 dd, MNHN;
KANADEEP: stn DW4945, 25°22'S, 159°43'E, 108-130 m, 3 dd, MNHN.

Vanuatu. MUSORSTOM 8: stn DW964, 20°20'S, 169°49'E, 360-408 m, 1 dd; stn DW1101, 15°04'S, 167°08'E, 205-210 m, 1 dd; stn CP1133, 15°39'S, 167°03'E, 174-210 m, 1 dd;
SANTO: Pleistocene of Santo, Kere River, near Finmele (site 1), 15°33'S, 166°57'E, coarse detrital level, 5 specimens.

Wallis & Futuna. MUSORSTOM 7: Futuna, stn DW496, 14°20'S, 178°04'W, 250-330 m, 1 dd; Field Bank, stn DW594, 12°31'S, 174°20'W, 495-505 m, 1 dd.

Tonga. BORDAU 2: stn DW1508, 21°02'S , 175°19'W, 555-581 m, 1 dd, IM-2008-965; stn DW1512, 21°19'S , 175°01'W, 183-184 m, 1 dd, IM-2008-963; stn DW1521, 21°19'S , 175°01'W, 225-233 m, 1 dd, MNHN-IM-2008-966; stn DW1567, 21°02'S, 175°19'W, 351-356 m, 1 dd, IM-2008-964; stn DW1603, 22°12'S , 175°20'W, 189-196 m, 3 dd, MNHN-IM-2008-967.

Distribution. New Caledonia, Vanuatu, Futuna and Tonga, living at 100-505 m, but most living specimens were collected between 230 and 265 m (Fig. 14).

Description. Shell medium sized for the genus, up to 17.3 mm in length at maturity (paratype MNHN-IM-2000-34208). Length/width ratio 2.0-2.1. Slender, lanceolate, narrowly ovate, heavy, nodose. Subsutural ramp broad, strongly sloping, weakly concave.
White or light tan, usually with spiral cords topped with brown; occasionally pure white. Siphonal canal brown or light brown and darker on tip. Aperture white.
Spire high with 3.5 protoconch whorls and teleoconch up to 5 broadly ovate, convex, weakly shouldered, nodose whorls. Suture adpressed. Protoconch small, conical with a very narrow keel abapically. Whorls smooth, glossy, height and width 900 µm. Terminal lip erect, of sinusigera type.
Axial sculpture of teleoconch whorls consisting of high, strong, broad, rounded, nodose ribs. First whorl with 9 ribs, second and third with 9 or 10, fourth with 9-11, last whorl with 8 or 9 ribs. Spiral sculpture of low, rounded, narrow, smooth, primary, secondary

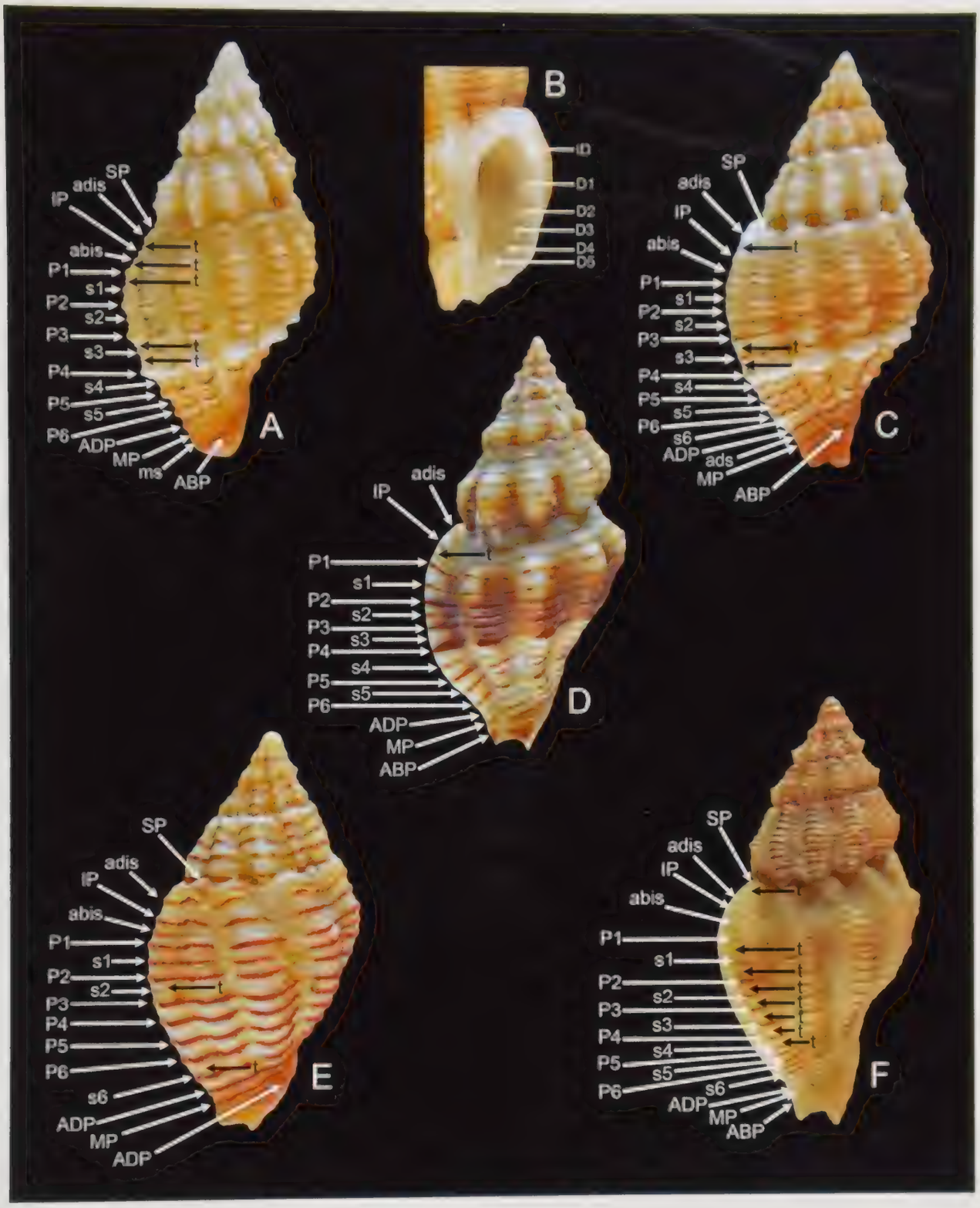


Figure 10 – Spiral sculpture and apertural morphology

A-B. *Cytharomorula arta* n. sp., Reunion, MD32, stn DC56, 21°05' S, 55°12' E, 1982, 170-225 m. A. Paratype MNHN-IM-2000-34205, 12.3 mm; B. Holotype MNHN-IM-2000-34203, 14.3 mm.
C. *Cytharomorula elegantula* n. sp., New Caledonia, Kaimon Maru Bank, SMIB 8, stn DW159, 28/01/1993, 24°46' S, 168°08' E, 241-245 m, paratype MNHN-IM-2000-34209, 15.7 mm.
D. *Cytharomorula grayi* (Dall, 1889), Canary Islands, Tenerife, Palma, in shrimp nets, 150-200 m, 1985, RH, 19.6 mm.
E. *Cytharomorula fatuhivaensis* n. sp., French Polynesia, Marquesas Islands, Fatu Hiva, 03/09/1990, 10 31' S, 138°39' W, 210 m, holotype MNHN-IM-2012-18829, 14.7 mm.
F. *Cytharomorula springsteeni* Houart, 1995, Philippines, tangle nets, 146 m, paratype RH, 12.7 mm.

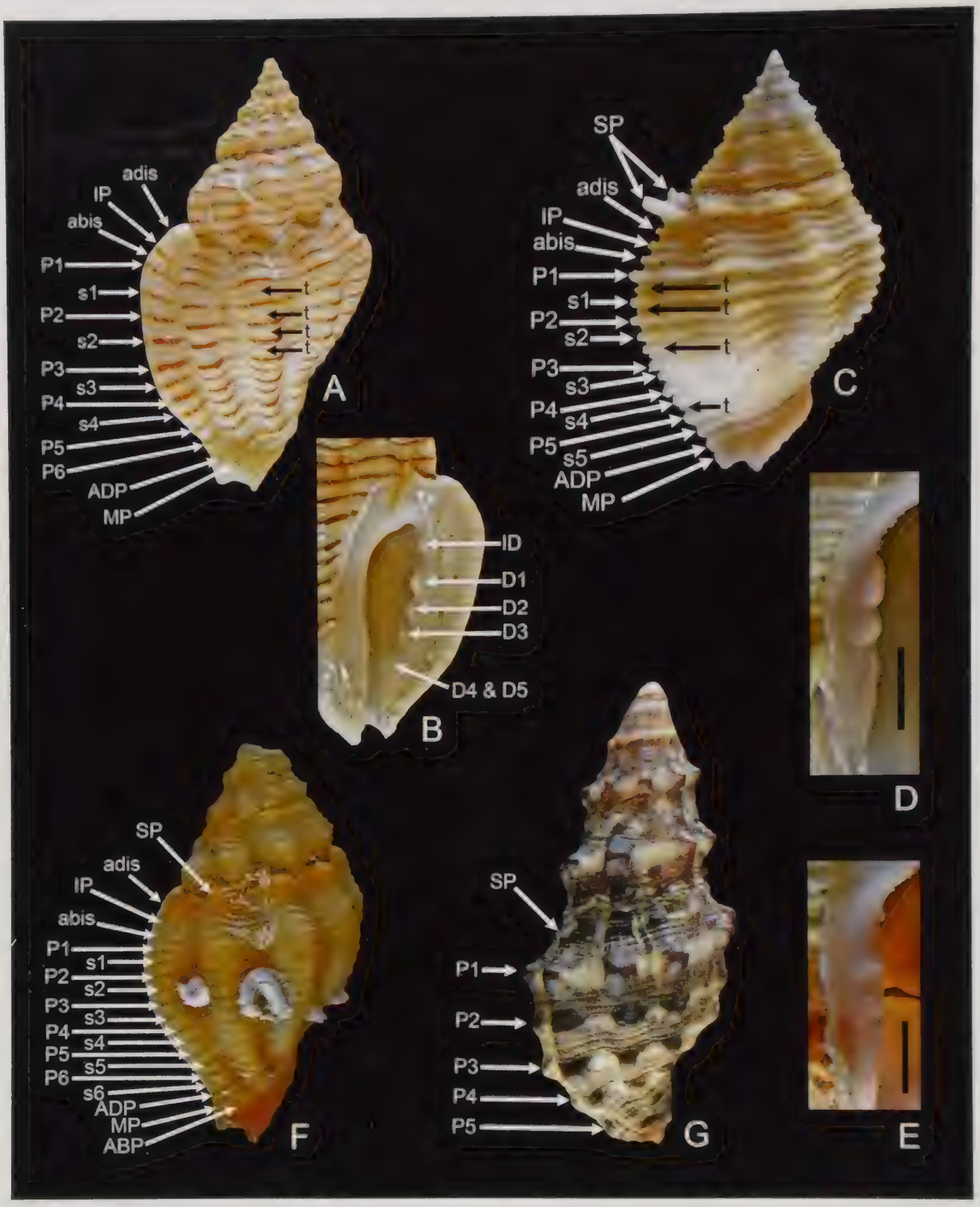


Figure 11 – Spiral sculpture and apertural morphology

A-B. *Cytharomorula grayi* (Dall, 1889), MD208, stn DW4877, Walters Shoal, 33°10'S, 43°49'E, 217-256 m, MNHN-IM-2013-66419, 23.2 mm.
C-D. *Orania pseudopacifica* n. sp., French Polynesia, Marquesas Islands, Nuku Hiva, 25/08/1997, 8°45' S, 140°13' W, 104-109 m, holotype MNHN-IM-2000-34211, 14.5 mm; D. Detail of the columella. Scale bar: 1 mm.
E. *Orania pacifica* (Nakayama, 1988), Philippines, Panglao, 55-81 m, detail of the columella, RH. Scale bar: 1 mm.
F. *Cytharomorula absidata* n. sp., New Caledonia, NORFOLK 2, stn DW2123, 23°18'S, 168°15'E, 187-197 m. Holotype MNHN-IM-2000-34201, 9.6 mm.
G. *Claremontiella adiakritos* n. sp., West Mexico, Mazatlan, holotype NHMUK 20180545, 23.3 mm.

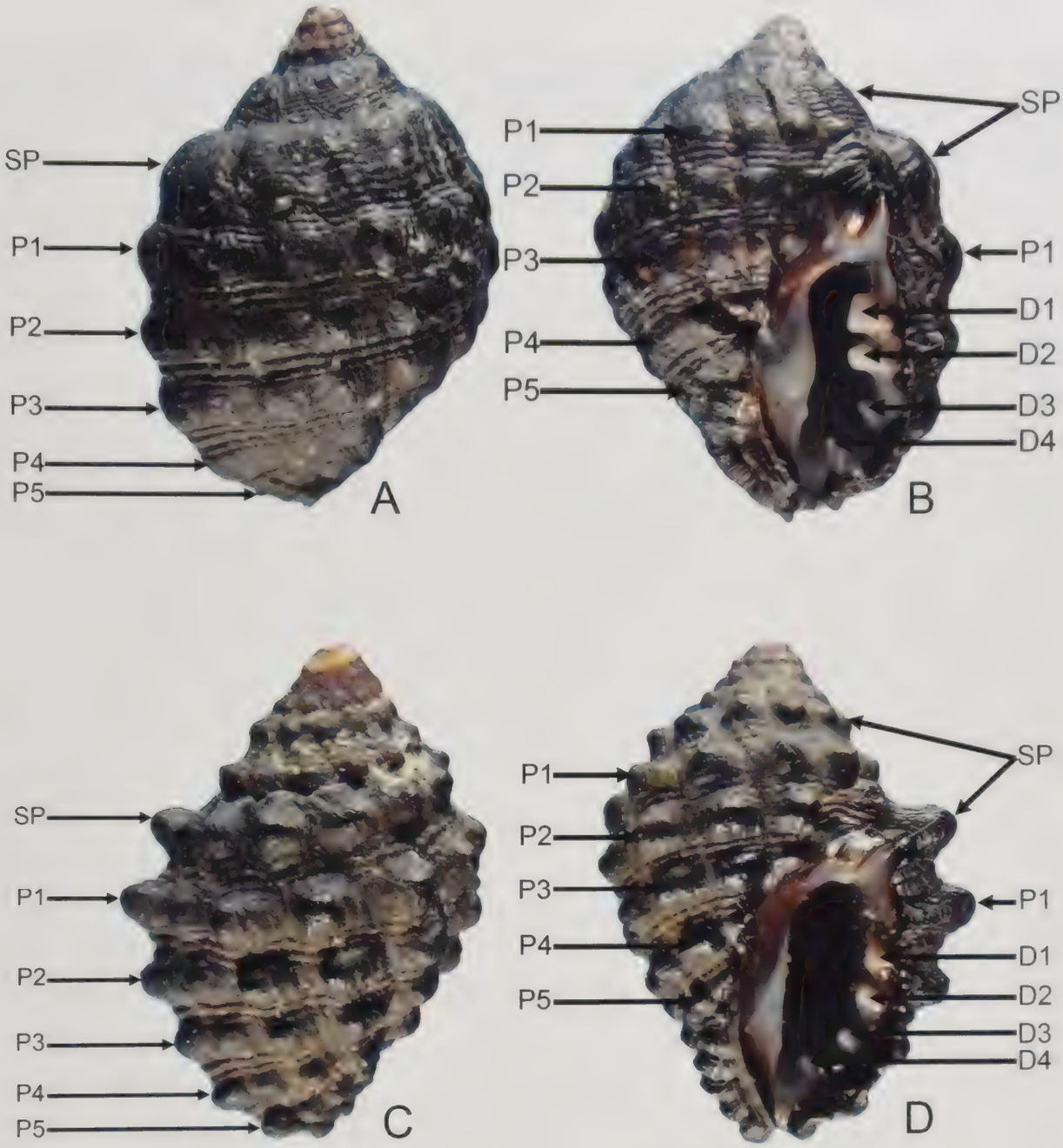


Figure 12 – Spiral sculpture and apertural morphology

A-B. *Tenguella chinoi* n. sp., Papua New Guinea, Papua Niugini, stn PR214, 08/12/2012, 1-8 m (no other information), MNHN, 12.5 mm.
C-D. *Tenguella ericius* n. sp., Vanuatu, SANTO, stn FM36, 15°22,4'S 167°13'E 27/09/2006 0-1 m, paratype MNHN-IM-2000-34218, 13.9 mm.

and tertiary cords. First teleoconch whorl with visible SP, IP, P1 and P2; second whorl with SP, adis, IP, P1, s1, P2, s2; third and fourth with additional abis and tertiary cords. Last whorl with SP, adis, IP, abis, P1, s1, P2, s2, P3, s3, P4, s4, P5, s5, P6, s6, ADP, ads, MP and ABP; P4 occasionally broader and higher with high knobs at intersection with axial ribs, then usually lighter or white coloured.

Aperture narrow, ovate. Columellar lip narrow with weak, low parietal tooth at adapical extremity and 2 or 3 elongate, low, narrow folds abapically. Rim weakly partially erect, adherent at small portion at adapical extremity. Anal notch deep, broad. Outer lip erect, smooth with 6 weak, low, elongate denticles within, consisting of ID, D1-D5. Siphonal canal short, 16-

18% of total shell length, narrow, dorsally recurved, broadly open.
Operculum unknown. Radula with three dimensional rachidian tooth bearing a long, narrow, projecting central cusp, a small, narrow lateral denticle on each side, a medium sized lateral cusp, as broad as central cusp but shorter, and a few marginal folds. No marginal cusps. Lateral teeth sickle shaped, relatively broad.

Remarks. *Cytharomorula grayi*, with which *C. elegantula* n. sp. has often been confused, differs in having a more strongly shouldered, less fusiform shell with a narrower, more concave and less strongly sloped subsutural ramp, and broader, stronger, higher axial ribs, broader and more obvious on shoulder. These axial ribs are also less numerous, 6 or 7 on the last teleoconch whorl in *C. grayi* as opposed to 8 or 9 in *C. elegantula* n. sp. *C. grayi* also has a broader, less fusiform aperture with more obvious denticles.
For differences with *Cytharomorula absidata* n. sp., *C. arta* n. sp. and *C. fatuhivaensis* n. sp. see the descriptions of these species herein.
The Pleistocene specimens from Vanuatu were collected during an exploration in February 2006 of fossil sites as part of the SANTO 2006 Expedition (Lozouet et al. 2011). The fossil specimens come from the Kere 1 deposit (= Kere Shellbed of Mallik and Ladd). A well-preserved coral (*Flabellum* sp.) collected in this outcrop gave an age of 133 000 yr. (Lozouet et al., 2011) (see also Houart, 2013b).

Etymology. *Elegantula* (L): diminutive of *elegans*, meaning small and elegant.

Cytharomorula fatuhivaensis n. sp.
Figs 10E; 14; 18A-F

Cytharomorula sp. cf. *C. grayi* — Tröndlé & Houart, 1992: 88, fig. 48 [(not *C. grayi* (Dall, 1889)].

Cytharomorula grayi — Houart & Tröndlé, 2008: 70, 92 [(not *C. grayi* (Dall, 1889)].

Type material. Holotype MNHN-IM-2012-18829, French Polynesia, Marquesas, Fatu Hiva, SMCB: stn CAS303, 10°31'S, 138°39'W, 210 m, lv.
Paratypes: French Polynesia, Marquesas, Fatu Hiva, 10°31'S, 138°39'W, 210 m, 16 lv, MNHN-IM-2000-34210, 1 lv, RH.

Type locality. French Polynesia, Marquesas, Fatu Hiva, 10°31'S, 138°39'W, living at 210 m.

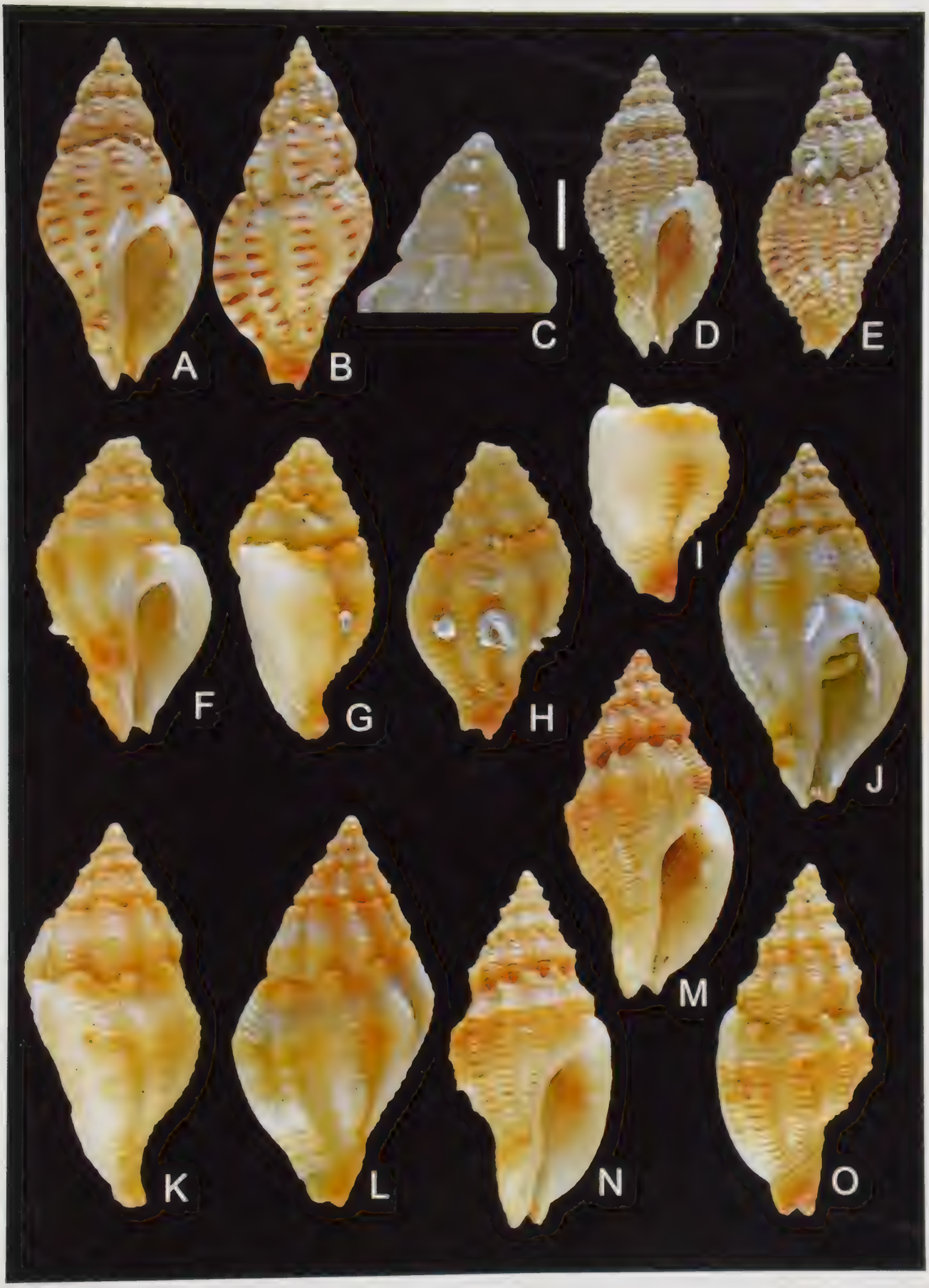
Other material examined. MUSORSTOM 9, stn DW1145, Marquesas, Ua Pou, 9°19'S, 140°06'W, 150-180 m, MNHN-IM-2008-2929, 7 lv & dd; stn DW1146, 9°19'S, 140°06'W, 200 m, MNHN-IM-2008-2928, 3 dd; stn DW1148, 9°19'S, 140°06'W, 300 m, MNHN-IM-2008-2927, 2 dd; stn DW1197, Hiva Oa, 9°57'S, 140°02'W, 277-372 m, MNHN-IM2008-2926, 1 dd; stn DR1247, Fatu Hiva, 10°34'S, 138°42'W, 1150-1250 m, MNHN-IM-2008-2925, 1 dd.

Distribution. French Polynesia, Fatu Hiva, Ua Pou and Hiva Oa, living at 180-210 m (Fig. 14).

Description. Shell medium sized for the genus, up to 16.5 mm in length at maturity (paratype MNHN). Length width ratio 1.8-2.0. Biconical, broadly ovate, heavy, nodose. Subsutural ramp broad, strongly sloping, weakly concave.
Light tan or whitish with dark brown spiral cords. Aperture white.
Spire high with 3.5 protoconch whorls and teleoconch up to 5 broad, strongly convex, weakly shouldered, nodose whorls. Suture strongly adpressed. Protoconch small, conical. Whorls smooth, glossy, with a very narrow keel abapically. Height and width 1000 µm. Terminal lip erect, of sinusigera type.

Figure 13 (scale bar: 500 µm)

A-C. *Cytharomorula vexillum* Kuroda, 1953.
A-B. Japan, Tosa, 128 m, MNHN, 21.1 mm; C. Protoconch, New Caledonia.
D-E. *Cytharomorula ornamentata* (Houart, 1995), South Africa, Durban, RH, 16.8 mm.
F-L. *Cytharomorula absidata* n. sp.
F-H. New Caledonia, NORFOLK 2, stn DW2123, 23°18'S, 168°15'E, 187-197 m, holotype MNHN-IM-2000-34201, 9.6 mm; I. New Caledonia, NORFOLK 2, stn DW2123, 23°18'S, 168°15'E, 187-197 m, paratype MNHN-IM-2007-18225 (BOLD MUBA765-18; GenBank HE584051.1) (fragment of analysed specimen, 8 mm); J-L.New Caledonia, SMIB 5, stn DW93, 22°20'S, 168°43'E, 240-255 m, paratype MNHN-IM-2000-34202, 13.7 mm.
M-O. *Cytharomorula springsteeni* Houart, 1995
M. Philippines, tangle nets, 146 m, paratype RH, 12.7 mm; N-O. New Caledonia, Kaimon Maru Bank, SMIB 8, stn DW159, 28/01/1993, 24°46' S, 168°08' E, 241-245 m, 13.2 mm, MNHN.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Axial sculpture of teleoconch whorls consisting of high, strong, broad, rounded, nodose ribs. First and second teleoconch whorls with 9 ribs, third with 8-10, fourth with 9 or 10 and last whorl with 6 or 7 ribs. Spiral sculpture of low, strong, narrow, nodose, primary, secondary and tertiary cords. First whorl with visible IP, P1, P2, starting s1; second whorl with SP; IP, P1, s1, P2, s2; third and fourth whorls with additional adis and occasionally with abis and tertiary cords. Last whorl with SP, adis, IP, abis, P1, s1, P2, s2, P3, P4, P5, P6, s6, ADP, MP and ABP and few tertiary cords (Fig. 10E). Primary and secondary cords of approximately similar size.

Aperture moderately small, narrow, ovate. Columellar lip moderately broad with weak, low parietal tooth at adapical extremity. Rim adherent or partially erect on a small portion abapically. Anal notch deep, broad. Outer lip erect, smooth, with 6 strong, elongate denticles within, decreasing in strength abapically, consisting of ID, D1-D5. Siphonal canal very short, 12-14% of total shell length, strongly dorsally bent, broadly open.

Operculum and radula unknown.

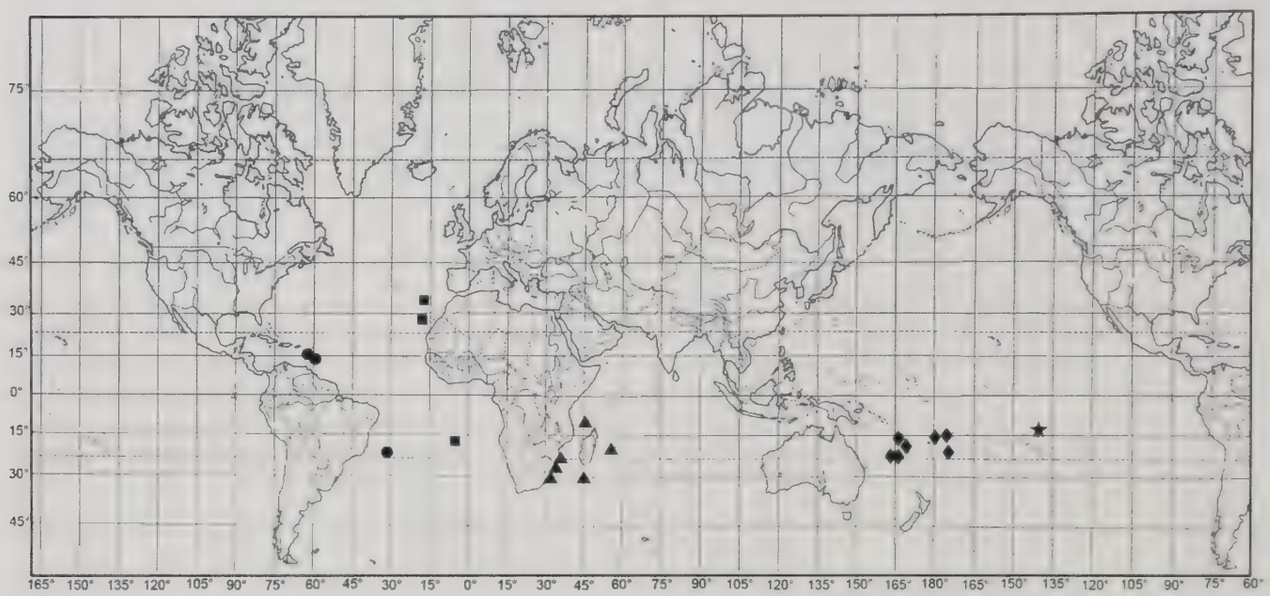
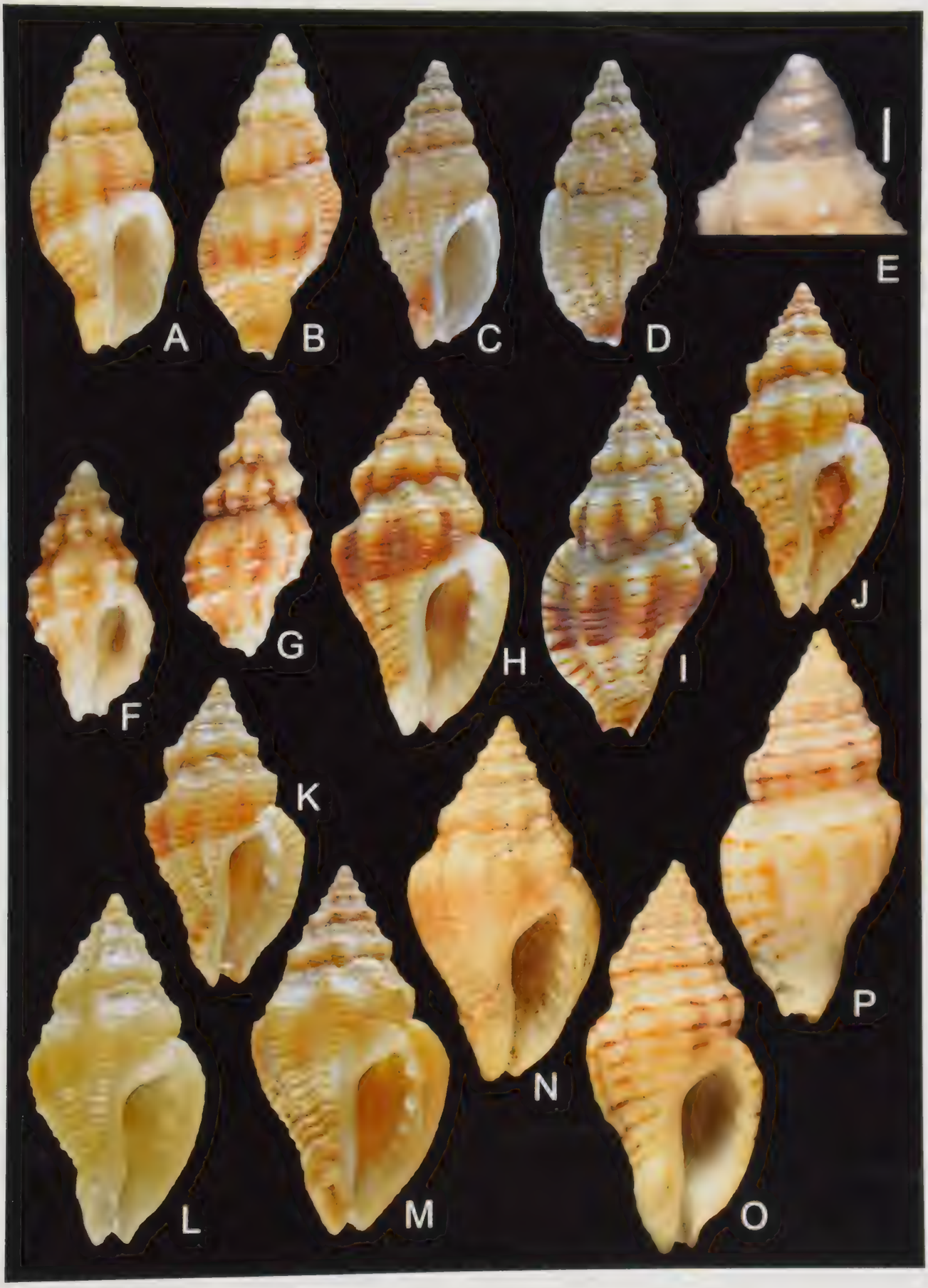


Figure 14. Distribution of the species in the *Cytharomorula grayi* group.
Cytharomorula grayi (●western Atlantic Ocean; ■eastern Atlantic Ocean;▲ western Indian Ocean); ◆ *C. elegantula* n. sp.; ★ *C. fatuhivaensis* n. sp.

Figure 15 (scale bar: 500 µm)

A-E. *Cytharomorula arta* n. sp.
A-B. Reunion, MD32, stn CP57, 21°05' S, 55°11' E, 1982, 210-227 m, holotype MNHN-IM-2000-34203, 14.3 mm; C-D. Reunion, MD32, stn CP57, 21°05' S, 55°11' E, 1982, 210-227 m, paratype MNHN-IM-2000-34206, 11.9 mm; E. Protoconch, Reunion, MD32, stn DC2, 1982, 21°12' S, 55°49' E, 160-190 m, paratype MNHN-IM-2000-34204.
F-G. *Cytharomorula lefevreiana* (Tapparone Canefri, 1880), MD32, Stn DC85, Reunion, 20°59' S, 55°15' E, 58-70 m, MNHN, 6.6 mm.
H-P. *Cytharomorula grayi* (Dall, 1889)
H-I. Canary Islands, Tenerife, Palma, in shrimp nets, 150-200 m, RH, 19.6 mm; J. East of Guadeloupe, south of Desirade, 250 m, RH, 13.8 mm; K. West coast of Barbados, dredged 165 m, RH, 13.2 mm; L South-Eastern Brazil, Martin Vaz Id, 20°32' S, 28°52' W, 780-795 m (dd), MNHN-IM-2012-33133, 14.1 mm; M. Madeira, RH, 17.8 mm; N. *Trophon lowei* Watson, 1897, Madeira, lectotype NHMUK 1911.7.17.2, 19.3 mm, photo Harry Taylor, NHMUK Photographic Unit, © Natural History Museum of London; O-P. *Cantharus laevis* E.A. Smith, 1890, St Helena, lectotype NHMUK 1889.10.1.2362, 22.2 mm, photo Harry Taylor, NHMUK Photographic Unit, © Natural History Museum of London.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Remarks. *Cytharomorula elegantula* n. sp. from New Caledonia (Fig. 16H-N), also described herein, differs from *C. fatuhivaensis* n. sp. in having a usually lighter, narrower shell, with a length/width ratio of 2.0-2.1 as opposed to the 1.8-2.0 of *C. fatuhivaensis* (*C. fatuhivaensis* is stockier and broader); in having a narrower and longer siphonal canal, 16-18% of total shell length, *vs* 12-14 % in *C. fatuhivaensis*; a higher, more elongate spire; narrower, lower, usually more numerous axial ribs; a comparatively more elongate aperture; less apparent, usually narrower spiral cords, except for P4 which is very often higher and more apparent in *C. elegantula* than has been observed in other *Cytharomorula* species, but which is of equal height to other cords in *C. fatuhivaensis*.

Etymology. Named after Fatu Hiva Island, the type locality.

***Cytharomorula manusuduirauti* n. sp.**
Figs 17; 18G-L

Cytharomorula pinguis — Tsuchiya, 2000: 381, pl. 189, fig. 88; Houart, 2008: 23, 198, pl. 394, fig. 6 [not *C. pinguis* Houart, 1995)]
Cytharomorula springsteeni — Tsuchiya, 2017: 954, pl. 247, fig. 4 [not *C. springsteeni* Houart, 1995)].

Type material. Holotype HMNS 2017.2223 Po.406866, Philippines, Aliguay Island, near 8°44' N, 123°12'E, sand, sandy gravel & sandy mud bottoms, 50-150 m, lv.
Paratypes: Philippines, Balicasag Island, near 9°31' N, 120°41'E, tangle or lumun-lumun net, 100-150 m, lv, 1 HMNS 2017.2223 Po.524523; Philippines, Balicasag Island, near 9°31' N, 120°41'E, tangle or lumun-lumun net, 50-80 m, dd, 1 HMNS 2017.2223 Po.571785; Philippines, Aliguay Island, rocky mud, 160 m, lv, 1 RH.

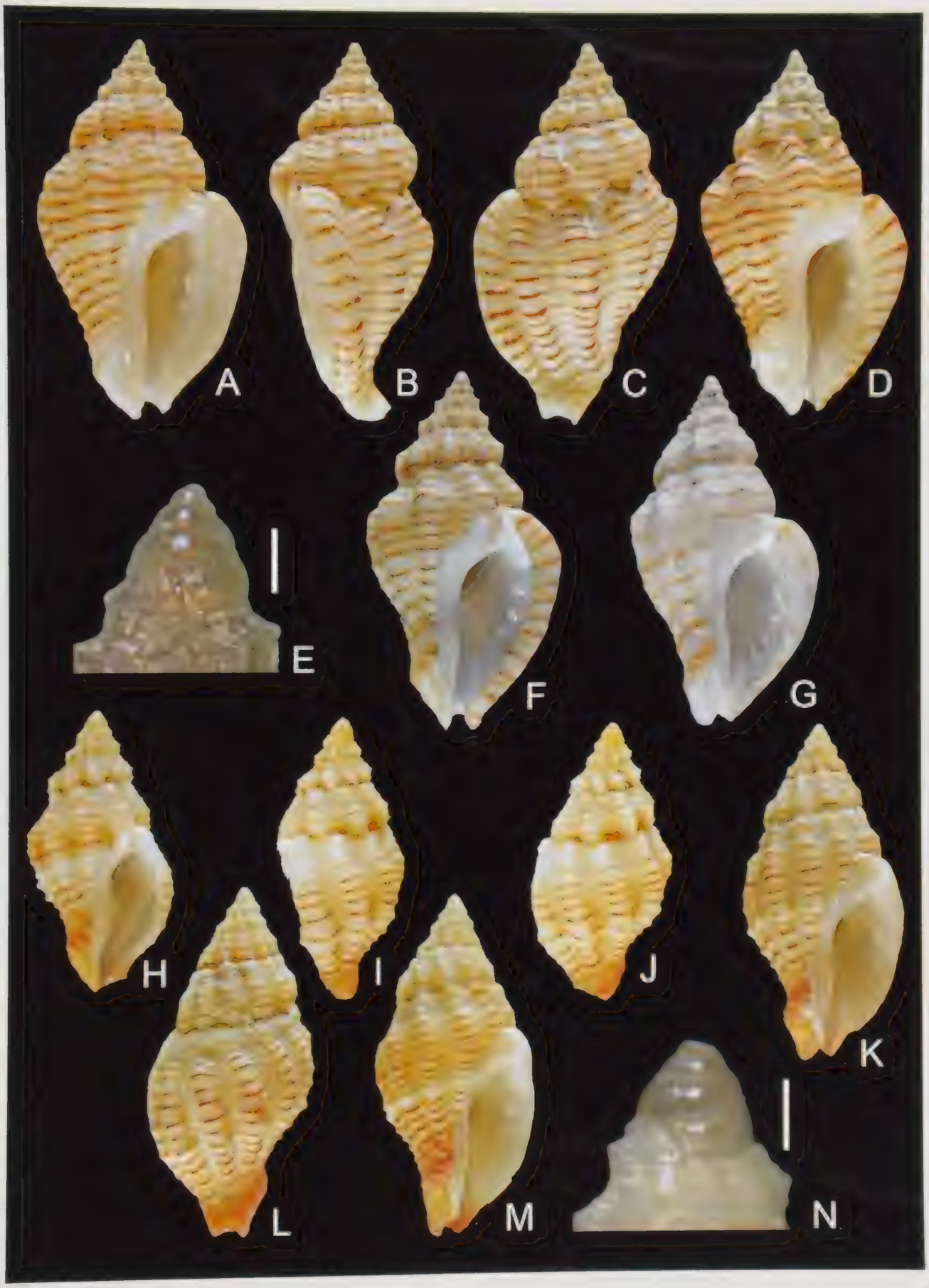
Type locality. Philippines, Aliguay Island, near 8°44' N, 123°12'40'E, sand, sandy gravel & sandy mud bottoms, 50-150 m.

Distribution. Philippines Islands, living at 150-160 m and Japan, Ogasawara Islands (Tsuchiya, 2017) (Fig. 17).

Description. Shell small, up to 11.6 mm in length (holotype). Length/width ratio 1.9-2.0. Biconical, broadly ovate, heavy, lightly nodose.
Light tan, extreme abapical part of last teleoconch whorl and siphonal canal dark brown or blackish brown. Occasionally with weak brown blotches between axial ribs of last teleoconch whorl. Aperture white, columellar lip occasionally with brown blotch abapically.
Spire high with 3+ protoconch whorls (first whorl broken) and teleoconch of 4 or 4.5 broad, weakly shouldered, nodose whorls, spire whorls more strongly shouldered. Suture adpressed.
Protoconch large, high, conical, glossy. Maximum width 800 µm, height 1000 µm. Terminal lip of sinusigera type.
Axial sculpture of teleoconch whorls consisting of moderately high, broad, rounded ribs, with 8 or 9 ribs on all whorls, ribs obviously broader on last whorl. Spiral sculpture of numerous, narrow, rounded cords, more than 35 on last whorl, equally distant and of same strength on whole length of shell.
Aperture small, ovate. Columellar lip narrow, smooth or with two weak, narrow knobs abapically. Rim weakly erect abapically, adherent adapically. Anal notch deep, broad. Outer lip smooth, with 6 strong, elongate denticles within, decreasing in strength abapically, consisting of ID, D1-D5. Siphonal canal very short, 8-10% of total shell length, narrow, weakly dorsally recurved, broadly open.
Operculum and radula unknown.

Figure 16 (scale bars: 500 µm)

A-G. *Cytharomorula grayi* (Dall, 1889)
A-D. MD208, stn DW4877, Walters Shoal, 33°10'S, 43°49'E, 217-256 m; A-C. MNHN-IM-2013-66419 (BOLD MUBA781-18; GenBank MK216540), 23.2 mm; D. MNHN-IM-2013-66418, 22.0 mm; E. Protoconch, Walters Shoal, MD208, stn DW4894, 33°09'S, 43°50'E, 199-261 m, MNHN; F. South Africa, Durban, off Umlaas Canal, coarse rubble, 14/12/1983, 128 m, NM B6282, 19.2 mm; G. SW Grande Glorieuse Id, BENTHEDI, stn DS93, 07/04/1977, 11°33' S, 47°16' E, 480-550 m, MNHN, 17.2 mm.
H-N. *Cytharomorula elegantula* n. sp.
H-J. New Caledonia, KANACONO, stn DW4778, 23°03'S, 168°18'E, 170-248 m, holotype MNHN-IM-2013-63326, (BOLD MUBA780-18; GenBank MK216542), 10.2 mm; K-L. New Caledonia, N.O. "Jean Charcot" BIOCAL, stn DW66, 03/09/1985, 24°56 S, 168°22 E, 505-515 m, paratype MNHN-IM-2010-23359, 16.3 mm; M. New Caledonia, N.O. "Jean Charcot" BIOCAL, stn DW66, 03/09/1985, 24°56 S, 168°22 E, 505-515 m, paratype MNHN-IM-2010-23359, 16.3 mm; N. Protoconch, New Caledonia, Kaimon Maru Bank, SMIB 8, stn DW159, 28/01/1993, 24°46' S, 168°08' E, 241-245 m, paratype MNHN-IM-2000-34209.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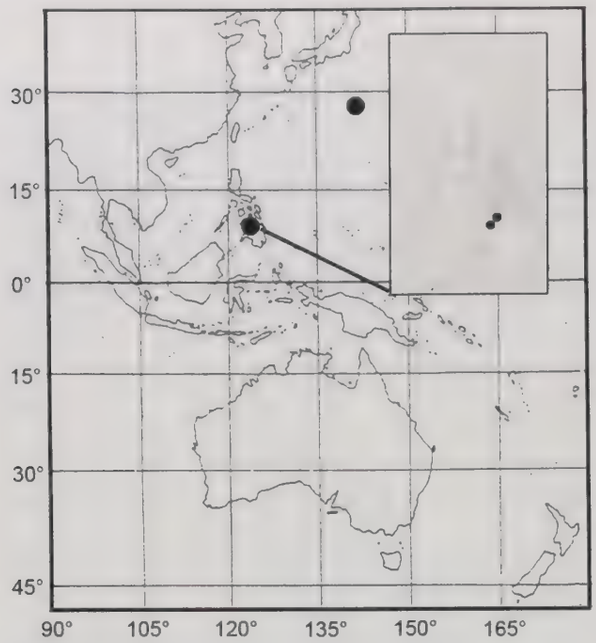

Figure 17. Distribution of *Cytharomorula manusuduirauti* n. sp.

Remarks. *Cytharomorula manusuduirauti* n. sp. has been confused with *C. pinguis* Houart, 1995 and *C. springsteeni* Houart, 1995. However both species differ from *C. manusuduirauti*.

Cytharomorula pinguis (Fig. 18M-N) differs in having a comparatively narrower shell with broader, flatter and less numerous spiral cords. *C. pinguis* also has a comparatively narrower aperture with strong D1 denticle and strong, heavy knobs on the columellar lip, as opposed to the smooth columellar lip with very weak adapical knobs in *C. manusuduirati* n. sp. Both species have primary, secondary and tertiary cords of approximately similar strength, which are difficult to separate. However, *C. pinguis* has 20-22 broad, flat cords on the last teleoconch whorl as opposed to 37-40 narrow, rounded cords in *C. manusuduirauti* n. sp.

Cytharomorula springsteeni (Fig. 13M-O) also differs from *C. manusuduirauti* n. sp. in many ways. The shell of *C. springsteeni* is narrower and more elongate, with a larger, higher aperture and a higher spire. The spiral sculpture also differs in being more irregular with higher, weakly broader primary and secondary cords compared to the narrower tertiary cords (Fig. 10F), rather than the similar sized, more numerous and crowded cords in *C. manusuduirauti* n. sp.

Etymology. Named for the late Emmanuel (Manu) Guillot de Suduiraut, friend and well-known shell enthusiast who sent a specimen (now paratype) of this new species to one of the authors (RH) several years ago.

Genus ***Orania*** Pallary, 1900

Type species by original designation: *Pseudomurex spadae* Libassi, 1859 (= *Murex fusulus* Brocchi, 1814), Mediterranean (Fig. 21A-C).

Diagnosis. Shell with high spire, elongate, ovate, nodose, not or rarely exceeding 25 mm in length at maturity. Axial sculpture of last teleoconch whorl consisting of 7-9 narrow, low, sharp or weakly rounded ribs. Spiral sculpture of low, narrow, primary, secondary and tertiary cords.

Aperture ovate, columellar lip weakly concave, smooth or with weak folds abapically, rim almost entirely adherent to shell. Anal notch broad, deep. Outer lip with strong, elongate denticles within. Siphonal canal short, broadly open ventrally.

Radula of the type species with three dimensional rachidian tooth bearing a long, moderately broad, projecting central cusp, a small, narrow lateral denticle, a moderately long, broad, lateral cusp and strong marginal folds giving rise to small, short marginal denticles, and a bifid marginal cusp. Lateral teeth sickle shaped, with broad base.

Figure 18 (scale bars: 500 µm)

A-F. *Cytharomorula fatuhivaensis* n. sp., French Polynesia, Marquesas Islands, Fatu Hiva, 03/09/1990, 10°31' S, 138°39' W, 210 m.

A-B. Holotype MNHN-IM-2012-18829, 14.7 mm; C. Protoconch, paratype MNHN-IM-2000-34210; D. Paratype MNHN-IM-2000-34210, 14.8 mm; E-F. Paratype MNHN-IM-2000-34210, 15.5 mm.

G-L. *Cytharomorula manusuduirauti* n. sp.

G-H. Philippines, Aliguay Island, near 8°44' N, 123°12'40' E, sand, sandy gravel & sandy mud bottoms, 50-150 m, holotype HMNS 2017.2223 Po.406866, 11.6 mm, photo Gary Kidder, The Houston Museum of Natural Science, Houston, Texas, U.S.A.; I. Philippines, Balicasag Island, near 9°31' N, 120°41' E, tangle or lumun-lumun net, 100-150 m, paratype HMNS 2017.2223 Po.524523, 10.1 mm, photo Gary Kidder, The Houston Museum of Natural Science, Houston, Texas, U.S.A.; J-L. Philippines, Aliguay Island, rocky mud, 160 m, paratype RH, 10.2 mm.

M-N. *Cytharomorula pinguis* Houart, 1995, New Caledonia, Loyalty Ridge, 20°41'S 167°07'E, 360 m, holotype MNHN-IM-2000-952, 16.7 mm, photo Manuel Caballer (MNHN) E-Recolnat Project: ANR-11-INBS-0004.

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Remarks. At present, 32 Recent species and one subspecies are assigned to *Orania* in WoRMS (MolluscaBase 2018). Of these, *O. ornamentata* Houart, 1995 is here transferred to *Cytharomorula*, and *O. albozonata* (E.A. Smith, 1890) is removed from Muricidae to the Buccinoidea (Pisaniidae).

One of the syntypes of *Cantharus albozonatus* E.A. Smith, 1890 in the NHMUK, most probably the shell figured by Smith (1890: 260, pl. 21 fig. 9), is here illustrated (Fig. 29I-J). That species is not a muricid but rather a buccinid close to *Enginella leucozona* (Philippi, 1844) (K. Fraussen, in litt.). However, based on the images we received from A. Salvador at the NHMUK, other buccinids are included in the 35 syntypes of *C. albozonatus* (see Fig. 29K-L), which is here tentatively assigned to *Enginella* Monterosato, 1917.

One new species of *Orania* is described herein, while *Muricopsis carnicolor* Bozzetti, 2009 (Figs 6E-F; 21D-H) and *Morula taiwana* are transferred to *Orania*. This leaves 33 species and one subspecies in this genus (Table 2).

The radula of *Orania fusulus* (Fig. 6G), the type species, is typical for the *Orania* type described in Houart (1995: 246, fig. 3), as it has broader cusps and denticles, small, short marginal cusps and a short marginal cusp. See also the radula of *Orania carnicolor* (Fig. 6E-F).

Orania pseudopacifica n. sp.

Figs 7A-B; 11C-D; 19; 20A-F

?*Morula* (?*Morula*) *pacifica* — Tröndlé & Houart, 1992: 102, fig. 81 [not *Orania pacifica* (Nakayama, 1988)].

Orania pacifica — Houart & Tröndlé, 2008: 92 [not *Orania pacifica* (Nakayama, 1988)].

Type material. Holotype MNHN-IM-2000-34211, MUSORSTOM 9, stn DW1170, French Polynesia, Marquesas Archipelago, Nuku Hiva, 8°45'S, 140° 10'W, 104-109 m, lv.

Paratypes: French Polynesia, Marquesas Archipelago, Nuku Hiva, MUSORSTOM 9, stn DW1170, 8°45'S, 140°, 10'W, 104-109 m, 10 lv, MNHN-IM-2000-34212, 2 lv, RH; stn CP1239, 09°42'S, 139°04'W, 89-95 m, 7 lv, MNHN-IM-2000-34213.

Type locality. French Polynesia, Marquesas Archipelago, Nuku Hiva, 8°45'S, 140°, 10'W, living at 104-109 m.

Other material examined. Marquesas Archipelago. MUSORSTOM 9: stn DW1144, 09°19'S, 140°04'W, 85-95 m, 6 lv & dd; stn DW1146, 09°19'S, 140°06'W, 200 m, 1 dd; stn DW1148, 09°19'S, 140°06'W, 300 m, 1 dd; stn DR1151, 09°19'S, 140°04'W, 70-77 m, 10 dd; stn DW1152, 07°59'S, 140°44'W, 85-150 m, 4 dd; stn CP1158, 07°59'S, 140°44'W, 109-110 m, 1 lv; stn CP1160, 07°58'S, 140°42'W, 49-55 m, 1 lv; stn DW1163, 08°57'S, 140°06'W, 78-85 m, 3 dd; stn DW1164, 08°58'S, 140°06'W, 170-180 m, 1 dd; stn DW1170, 08°45'S, 140°13'W, 104-109 m, 94 lv & dd; stn CP1177, 08°45'S, 140°14'W, 108-112 m, 3 dd; stn CP1178, 08°46'S, 140°15'W, 74-75 m, 2 dd; stn DR1181, numerous, specimens, 08°46'S, 140°03'W, 102-130 m, dd; stn DR1182, 08°46'S, 140°04'W, 90-120 m, 3 dd; stn 1183, 08°46'S, 140°04'W, 86-120 m, 2 dd; stn DR1200, 09°50'S, 139°09'W, 96-100 m, 6 dd; stn DW1208, 09°49'S, 139°10'W, 117 m, 2 lv & dd; stn DW1210, numerous specimens, 09°50'S, 139°01'W, 98-100 m, dd; stn DW1217, numerous specimens, 09°44,5'S, 138°50'W, 85-87 m, lv & dd; stn DR1223, 09°45'S, 138°51'W, 90-150 m, 7 dd; stn DW1224, numerous specimens, 09°45'S, 138°51'W, 115-120 m, dd; stn CP1227, numerous specimens, 09°44'S, 138°53'W, 84-85 m, lv & dd; stn CP1228, 09°45'S, 138°52'W, 107-108 m, 19 dd; stn DW1230, 09°44'S, 139°07'W, 95-100 m, 18 dd; stn DW1235, 09°42'S, 139°04'W, 105-285 m, 7 dd; stn CP1237, 09°42'S, 139°04'W, 95-305 m, 17 lv & dd; stn CP1239, 09°42'S, 139°04'W, 89-95 m, 26 lv & dd; stn DR1240, 10°25'S, 138°41'W, 70-90 m, 1 dd; stn DW1241, 10°28'S, 138°41'W, 85-130 m, 1 dd; stn DR1245, 10°29'S, 138°36'W, 85-130 m, 14 dd; stn DW1256, 09°25'S, 140°08'W, 70-72 m, 1 dd; stn DR1257, 09°26'S, 140°08'W, 85-127 m, 13 dd; stn DW1260, 09°25'S, 140°07'W, 49-100 m, 9 dd; stn CP1265, 09°20'S, 140°07'W, 90-92 m, 19 lv; stn DW1274, 07°55'S, 140°40'W, 100-120 m, 2 dd; stn DW1280, 07°59'S, 140°43'W, 87-98 m, 3 dd; stn DW1281, 07°48'S, 140°21'W, 450-455 m, 1 dd; stn DW1288, 08°54'S, 139°38'W, 200-220 m, 1 dd; stn DR1292, 08°54'S, 139°37'W, 95-100 m, 43 dd; stn DW1293, 08°54'S, 139°38'W, 50 m, 4 lv & dd; stn CP1294, 08°54'S, 139°38'W, 100 m, 4 lv; stn DR1297, 08°54'S, 139°37'W, 90-150 m, 1 lv; stn DR1298, 08°49'S, 140°17'W, 305 m, 3 dd; stn CP1304, 08°54'S, 140°14'W, 50-58 m, 2 dd; stn DR1305, numerous specimens, 08°54'S, 140°15'W, 90-155 m, dd.

Distribution. French Polynesia, Marquesas Archipelago, 7°48'S – 10°29'S, 138°36'W – 140°44'W, living at 50-117m (Fig. 19).

Description. Shell medium sized for the genus, up to 16.8 mm in length at maturity (paratype MNHN). Length/width ratio 1.7-1.8. Biconical, broadly-ovate, heavy, weakly nodose, finely squamous. Subsutural ramp broad, strongly sloping, weakly concave.

White, light tan or light peach. Aperture white, occasionally tinged with light pink at edge of columellar lip.

Spire high with 3.5-4 protoconch whorls and teleoconch of up to 5 broad, weakly shouldered whorls. Suture of whorls adpressed. Protoconch small, conical, acute. Whorls smooth, glossy, with a very narrow, single keel abapically. Height 900 µm, width 750-800 µm. Terminal lip of sinusigera type.

Axial sculpture of teleoconch whorls consisting of low, broad, rounded ribs. First and second teleoconch whorls with 7-9 ribs, third with 8 or 9, fourth with 7 or 8, last whorl with 6 or 7 ribs. Spiral sculpture of high, rounded, narrow, finely squamous, primary, secondary and tertiary cords and few additional narrow threads. First whorl with SP, IP, P1, second whorl with SP, IP, starting abis, P1, s1, third with SP, starting adis, IP, abis, P1, t, s1, fourth with SP, adis, IP, abis, P1, t, s1, last teleoconch whorl usually with SP, adis, IP, abis, P1, t, s1, t, P2, s2, t, P3, s3, P4, s4, t, P5, s5, ADP, MP and one or two additional threads. SP sometimes split, broad, strongly squamous, occasionally with high, projecting scales.
Aperture moderately large, narrow, ovate. Columellar lip narrow with 2-4 strong knobs on whole length, deeply extended within aperture (Fig. 11D). Rim partially erect, adherent at small portion adapically. Occasionally with weak, low parietal tooth at adapical extremity. Anal notch deep, broad, with expanded lip. Outer lip erect, crenulated, with 6 strong, elongate denticles within, decreasing in strength abapically, consisting of ID, D1-D5. Siphonal canal short, broad, dorsally recurved, broadly open.
Radula of three-dimensional type consisting of a rachidian with a narrow, long central cusp, a short lateral denticle and a fairly broad, moderately long lateral cusp on each side, few, obvious, marginal folds and a very short, broad, marginal cusp. Lateral teeth sickle shaped with broad base and narrow extremity.

Remarks. *Orania pseudopacifica* n. sp. may be compared with only three species: *O. pacifica* (Nakayama, 1988), with which it was confused in recent literature, *O. rosea* Houart, 1996 and *O. pleurotomoides* (Reeve, 1845).
Orania pacifica (Figs 7C; 11E; 20G-H) differs in having a more strongly squamous shell with a less obvious subsutural primary cord (SP); a narrower subsutural ramp; and differently-arranged, narrower and weaker columellar folds, which are less deeply extended within the aperture (Fig. 11E). The anal notch is also narrower in *O. pacifica,* with a less expanded lip. *Orania pacifica* is widely distributed in the Indo-West Pacific, from Japan (type locality), Taiwan, the Philippines, and several other localities in the Indo-West Pacific, to Mozambique and South Africa in the Indian Ocean.
Orania rosea (Fig. 20K-N), described from Reunion Island in the Indian Ocean but also found in the Philippines grows much larger, up to 23-25 mm in length, is more fusiform with a more squamous shell. The aperture is obviously larger and comparatively more strongly ovate, with a relatively smooth columellar lip except for the low abapical folds. It also has a less obvious subsutural cord.
Orania pleurotomoides (Fig. 20I-J) has a more strongly shouldered shell with a less bent, narrower subsutural ramp; a narrower subsutural cord; and much narrower or absent secondary cords. In this species, the last teleoconch whorl is more sharply bent anteriorly while the siphonal canal is obviously narrower. The aperture is more triangular with a series of low abapical folds decreasing in strength abapically; a narrow, more obvious parietal tooth and a narrower anal notch with a less expanded lip.
To my knowledge, none of these three species occur in French Polynesia.

Etymology. *Pseudo* (G) = false. Named *pseudopacifica* because it was misidentified as *Orania pacifica* in recent literature.

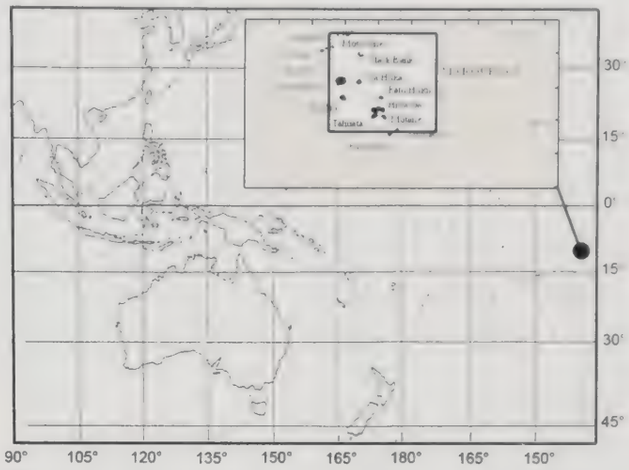


Figure 19. Distribution of *Orania pseudopacifica* n. sp.

Orania carnicolor (Bozzetti, 2009) comb. nov.
Figs 6E-F; 21D-H

Muricopsis carnicolor Bozzetti, 2009: 19, text figs.

Type material. Holotype MNHN-IM-2000-22900.

Type locality. South Madagascar, Lavanono, 280 kms southwest of Tolagnaro.

Other Material examined. Madagascar. ATIMO VATAE, stn TS02, 25°01.3'S, 47°00.5'E, 18 m, 1dd; stn BB03, 25°26.4'S, 44°56.1'E, 14-18 m, 3 lv, (MNHN-IM-2009-22465, MNHN-IM-2009-22485), 1 dd; stn BB04, 25°26.9'S, 44°55.9'E, 14-18 m, 5 lv & dd; stn BS04, 25°26.9'S, 44°55.9'E, 14-18m, 1 dd; stn TS04, 25°02.3'S, 47°00.3'E, 22-24 m, 2 dd; stn TB05, 25°02.2'S, 47°00.4'E, 23 m, 3 lv, 1 dd (MNHN-IM-2009-14481, MNHN-IM-2009-22445); BP06, 25°25.4'S, 44°54.5-7'E, 19-20 m, 6 lv (MNHN-IM-2009-22501-05, MNHN-IM-2009-22511-12); stn BP07, 25°27.2-6'S, 44°55.6-9'E, 18-22 m, 4 dd; stn BP08, 25°27.3-6'S, 44°55.2'E, 25-26 m, 2 dd; stn BP10, 25°25.5-8'S, 44°54.4-6'E, 23-25 m, 4 lv & dd; stn TA10, 25°28.3'S, 44°55.6'E, 23 m, 1 dd; stn BS11, 25°28.6'S, 44°56.8'E, 8-11 m, 1 dd; stn BP21, 25°23.1-2'S, 44°51.4-6'E, 20-23 m (MNHN-IM-2009-22505); stn BP22, 25°23.4'S, 44°51.7'E, 20-22 m, 5 lv & dd; stn BP31, 25°23.6-7'S, 44°53.3-5'E, 10-12 m, 1 dd; stn BP33, 25°25.80-8'S, 44°55.7-8'E, 11-13 m, 4

lv & dd; stn TA35, 24°45.6'S, 47°12.4'E, 5-6 m, 1 lv, 1 dd, (MNHN-IM-2009-22441); stn BP36, 25°21.9'S, 44°50.2'E, 10-17 m, 1 lv; stn BP37, 25°22.4-7'S, 44°50.2-7'E, 19-20 m 1 lv, 1 dd; stn BP41, 25°22.9-23.2'S, 44°51.0-6'E, 19-21 m, 3 lv; stn BP42, 25°22.8-23.7'S, 44°51.1'E, 18-21 m, 10 lv & dd; stn CP3510, 25°14.6'S, 47°09.1'E, 79-80, 1 lv (MNHN-IM-2009-22439); stn DW3519, 24°51.9'S, 47°28.0'E, 80-83 m, 6 lv & dd; stn CP3545, 25°29'S, 46°42'E, 108-110 m, 1 dd; stn CP3546, 25°22.7'S, 46°42.5'E, 84-85 m, 5 lv & dd; stn CP3547, 25°18.0'S, 46°40.3'E, 69-70 m, 5 lv; stn DW3550, 26°03.2'S, 45°32.1'E, 98 m, 2 dd; stn CP3572, 25°11.7'S, 47°12.5'E, 75-77 m, 3 lv & dd; stn CP3579, 25°54.5'S, 45°33.2'E, 65-66 m, 1 lv, 1 dd; stn DW3606, 25°48.4'S, 44°51.1'E, 44-46 m, 17 dd; stn DW3608, 25°39.4'S, 44°53.0'E, 37-38 m, 16 lv & dd [MNHN-IM-2009-14366 (BOLD MUBA290-15; GenBank MK216552), MNHN-IM-2009-22448 (BOLD MUBA312-15; GenBank MK216545), MNHN-IM-2009-22449 (BOLD MUBA313-15; GenBank MK216557)]; stn DW3609, 25°34.3'S, 44°55.2'E, 32 m, 3 dd; stn CP3624, 25°38.1'S, 45°57.0'E, 63 m, 11 lv & dd; stn DW3626, 25°30.2'S, 45°46.3'E, 41-42 m, 1 dd.

Distribution. South Madagascar, living at 13-84 m.

Remarks. *Orania carnicolor* was described as a species of *Muricopsis*, a genus unknown in the Indo-West Pacific, based on three dead collected specimens, but the general shape of these shells are reminiscent of several species of *Orania*, including *O. fusulus*, the type species. Its assignment to Ergalataxinae is confirmed by the morphology of the radula, here illustrated for the first time (Fig. 6E-F).

Orania castanea (Küster, 1858)
Figs 6H; 21I-K

Purpura castanea Küster, 1858: 170, pl. 28, figs 8, 9.
Cominella fasciata Sowerby III, 1886: 3.
Cominella unifasciata var. *concolor* Sowerby III, 1897: 4.
Cominella unifasciata nigronodulosa Turton, 1932: 53, pl. 12, fig. 302.
Thais castanea (Krauss) — Barnard, 1974: 691.
Thais castanea — Kensley, 1973:146, fig. 507.
Thais castanea (Küster, 1886) — Barnard, 1959: 224; Richards, 1981: 56, pl. 29, fig. 230; Kilburn & Rippey, 1982: 89, pl. 20, fig. 7; Steyn & Lussi, 1998: 96, fig. 371.
Nucella castanea (Küster, 1886) — Houart et al., 2010: 197.

Type material. *Purpura castanea*: "There is no indication. The whereabouts of this type (even if from Kuster's coll.) are unknown. *P. castanea* was founded on material coming from F. Krauss, probably destroyed during the war in Stuttgart" (R. Janssen, in litt.); *Cominella fasciata*: three syntypes NHMUK 86.4.2.10; *Cominella unifasciata* var. *nigronodulosa*: one syntype Oxford Museum.

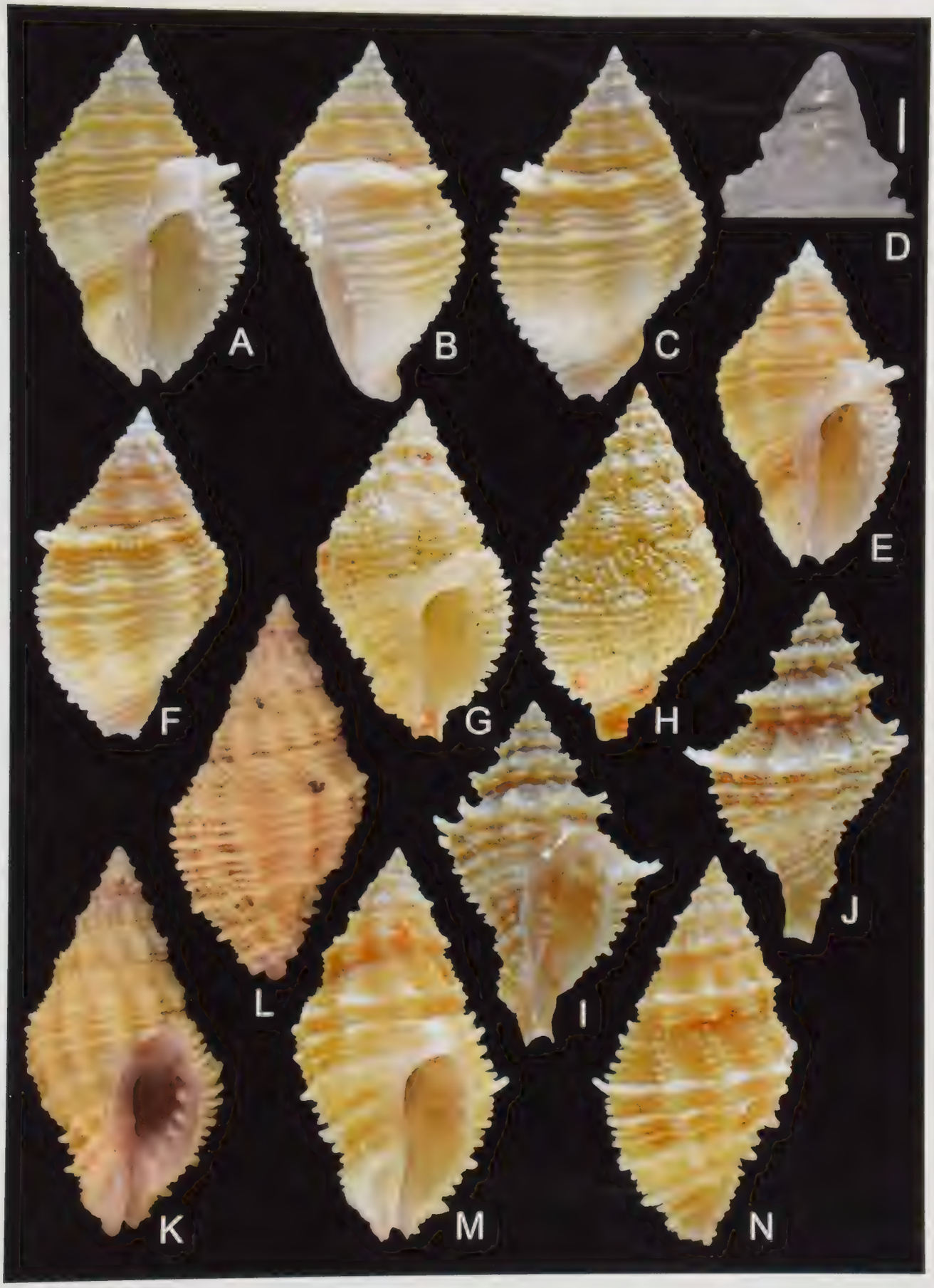
Type localities. *Purpura castanea*: Cape Agulhas; *Cominella fasciata*: Port Elizabeth; *Cominella unifasciata* var. *concolor*: Natal; *Cominella unifasciata nigronodulosa*: Port Alfred.

Distribution. South Africa, from False Bay to the south coast of Natal, and Walters Shoals, south of Madagascar, approximately 33°12'S, 43°50'E (new locality).

Other material examined. South Africa: W Cape Province, Witsand, 2 lv (RH); East London, 3 lv (RH) (radula illustrated); East Cape Province, WSW of East London, 6 lv (RH); Gonubie, East London, 1 lv (RH); Haga Haga, 3 lv & dd (RH); South Africa (no other data), 10 dd (RH).
Walters Shoal seamount: MD208: stn WS08, 33°14'S, 43°56'E, 30-33 m, MNHN-IM-2013-66431, 1 lv (BOLD MUBA784-18; GenBank MK216551); stn WS08, 33°14'S, 43°56'E, 30-33 m, MNHN-IM-2013-66432, (BOLD MUBA785-18; GenBank MK216550) 1 lv; stn WB09, 33°14'S, 43°56'E, 27-30 m, MNHN-IM-2013-66434, (BOLD MUBA786-18; GenBank MK216541), 1 lv; stn WB10, 33°09'S, 43°52'E, 30 m, MNHN-IM-2013-66424, (BOLD MUBA783-18; GenBank MK216555), 1 lv; stn WB10, 33°09'S, 43°52'E, 30 m, 2 lv.

Figure 20 (scale bar: 500 μm)

A-F. *Orania pseudopacifica* n. sp. French Polynesia, Marquesas Islands, Nuku Hiva, 8°45' S, 140°13' W, 104-109 m.
A-D. Holotype MNHN-IM-2000-34211, 14.5 mm; E-F. Paratype MNHN-IM-2000-34212, 14.0 mm.
G-H. *Orania pacifica* (Nakayama, 1988), Philippines, Balut Island, RH, 17.5 mm.
I-J. *Orania pleurotomoides* (Reeve, 1845), Philippines, Mactan Island, 60 m, RH, 16.1 mm.
K-N. *Orania rosea* Houart, 1996
K-L. Reunion Island, off Saint Pierre, 21°21'S 55°27'E, 73-77 m, holotype MNHN-IM-2000-910, 18.6 mm, photo Manuel Caballer (MNHN) E-Recolnat Project: ANR-11-INBS-0004; M-N. Philippines Mactan Id, Cebu, 120 m, sand and broken coral, RH, 20.9 mm.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Remarks. In Claremont et al (2013: 23, fig. 1; 24, fig. 2), subclade Z contains "*Thais*" *castanea*, which was well supported in a cluster with *Orania fischeriana* (Tapparone Canefri, 1882), *Orania pacifica* and *O. mixta* Houart, 1995, and we here confirm this result (Fig 3). "*Thais*" *castanea* is clearly not a member of any rapanine or ocenebrine genus, and should be reassigned to Ergalataxinae. This assignment is further confirmed by its radula morphology (Fig. 6H), which is similar to *Orania*.
The date of Küster's publication of the original description of *Orania castanea* is wrongly indicated as 1886 by numerous authors, including one of the us (RH) and in WoRMS (MolluscaBase 2018). This is probably due to Barnard (1959: 224), who was probably the first to make this mistake.
Six live specimens were collected during the recent MD 208 expedition to the Walters Shoal Mountain (Fig. 21K). This range extension, even if not unexpected in this area, remains very interesting.

Orania pachyrhaphe (E.A. Smith, 1879)
Fig. 22A-E

Fusus pachyrhaphe E.A. Smith, 1879: 205, pl. 20, figs 37, 37a.
Bedeva bireleffi — Tsuchiya, 2000: 381, pl. 189, fig. 90 [not *Bedevina birileffi* (Lischke, 1871)].

Type material. Lectotype NHMUK 1878.10.16.2/1, here designated; 1 paralectotype (*O. pachyrhaphe*) NHMUK 1878.10.16.2/2 and 3 paralectotypes (actually *B. birileffi*) 1878.11.7.28.

Type locality. Japan, Ukushima, Goto Islands, 33°15.5' N, 129°5'E, 11 fathoms (20 m) (station 8 in E.A. Smith, 1879: 182) (here selected).

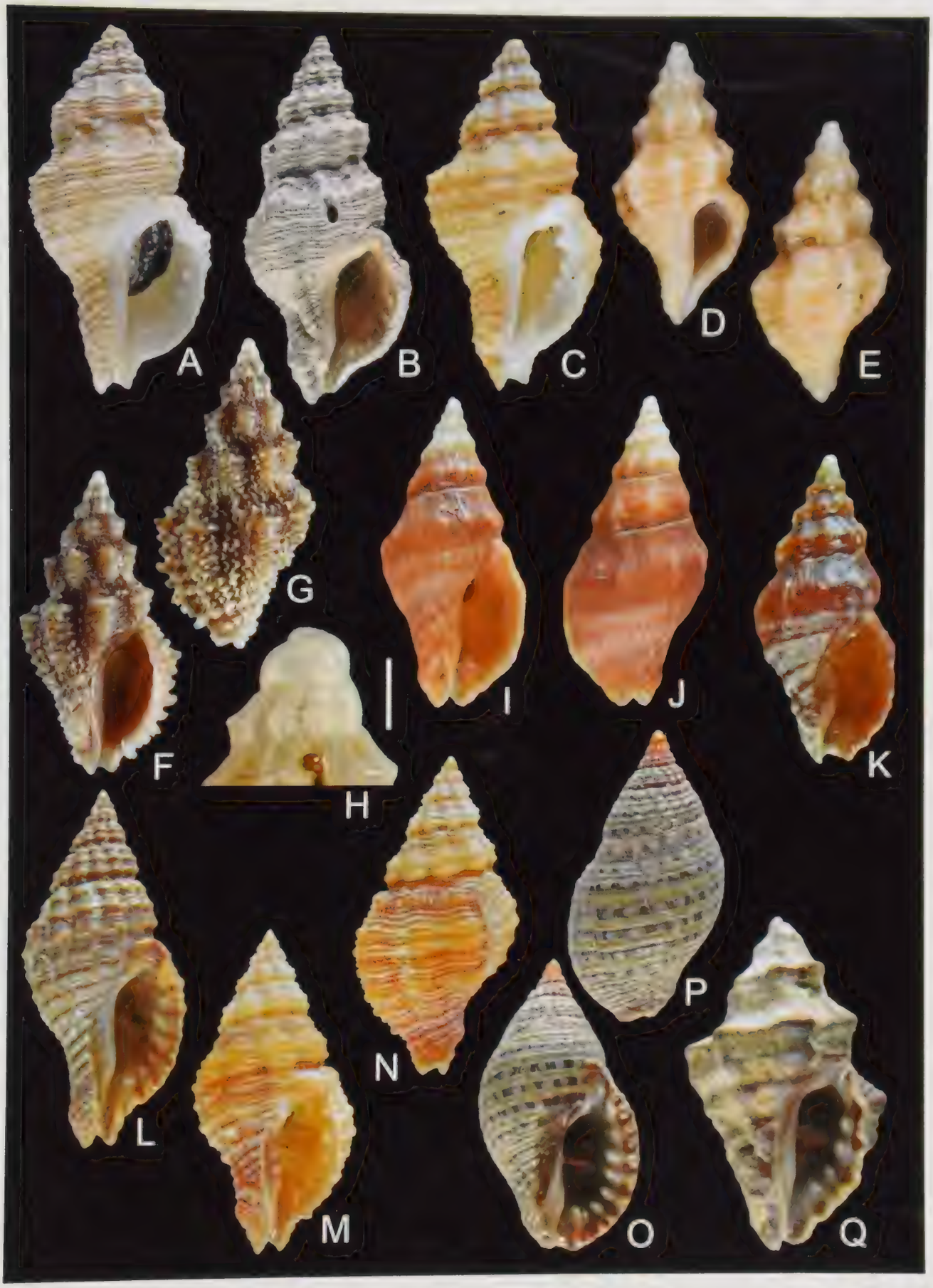
Material examined. Lectotype NHMUK and 4 paralectotypes; Japan, Okinawa, Haneji Inland Sea, on rocks, 0.3-1 m, lv, 13 RH.

Distribution. Japan, Okinawa and Goto Islands.

Remarks. Smith (1879: 205) mentioned two specimens in his description, one of 21 mm (illustrated in his plate 20, fig. 37) and one of 16 mm (his plate 20, fig. 37a). However, further in his text he wrote: "*The largest specimen from the latter locality differs from the rest...*" and "*I feel convinced that they all belong to one and the same species*". Thus we may conclude that more than two specimens were involved, and there are indeed five syntypes in NHMUK, of which two are the ones originally illustrated. However, the specimens illustrated by E.A. Smith belong to two different species. His fig. 37 is clearly the largest specimen deposited in NHMUK, here designated lectotype of *O. pachyrhaphe* (Fig. 22A-B), but his fig. 37a and two other paralectotypes are what is now known as *Bedevina birileffi* (Lischke, 1871), the intricate history of which was analysed by Houart et al. (2013). The smallest of the four paralectotypes is a young specimen of *O. pachyrhaphe* (Fig. 22C). A specimen of *B. birileffi* is here illustrated (Fig. 22H-I) together with the paralectotype figured by E.A. Smith (1879: fig. 37a) (Fig. 22F-G). *Bedevina* was analysed in Claremont et al (2013) and its validity in the Ergalataxinae was confirmed. However, the boundaries of this genus remain unclear because the same clade contained some species included in *Spinidrupa* (but not the type species). The definition of *Bedevina* and *Spinidrupa* thus remain to be delimited exactly, but, as noted in Claremont et al. (2013: 27), the conservative retention of both genera is recommended until further analyses are undertaken.

Figure 21 (scale bar: 500 µm)

A-C. *Orania fusulus* (Brocchi, 1814), A. Spain, Fuengirola, RH, 22.6 mm; B. Italy, Piacenza, Piacenziano, Castell'Arquato, Pliocene, RH, 23.2 mm; C. West Africa, Mauritania, RH, 17.4 mm.
D-H. *Orania carnicolor* (Bozzetti, 2009)
D-E. Madagascar, Lavanono, holotype MNHN-IM-2000-22900, 9.15 mm, photo Manuel Caballer (MNHN) E-Recolnat Project: ANR-11-INBS-0004; F-G. ATIMO VATAE, stn BP22, Madagascar secteur Ouest de Lavanono, 25°23.4'S, 44°51.7'E, 20-22 m, MNHN, 11.3 mm; H. Protoconch, ATIMO VATAE, stn CP3545, 25°29'S, 46°42'E, 108-110 m, MNHN.
I-K. *Orania castanea* (Küster, 1858)
I-J. South Africa, Haga Haga, RH, 13.5 mm; K. MD208, stn WB10, Walters Shoal, 33°09,1'S, 43°51,8'E, 30 m, MNHN-IM-2013-66424, (BOLD MUBA783-18; GenBank MK216555), 12.4 mm.
L. *Orania gaskelli* (Melvill, 1891), Papua New Guinea, Hansa Bay, RH, 16.6 mm.
M-N. *Orania serotina* (A. Adams, 1853), Philippines, Cebu, Mactan Id, Punta Engaño, RH, 14.3 mm.
O-P. *Usilla avenacea* (Lesson, 1842), Marquesas, Ua Huka, RH, 11.1 mm.
Q. *Orania bimucronata* (Reeve, 1846), Malaya, Tioman, RH, 14.6 mm.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Orania pachyrhaphe differs from *B. birileffi* in reaching a larger size relative to the number of teleoconch whorls; in having a lower spire; in having a spiral sculpture consisting of narrow primary cords together with weakly narrower secondary cords and small tertiary cords *versus* rounded, more crowded primary and secondary cords of approximately similar size; and in that adults specimens of *B. birileffi* lack tertiary cords. In addition, the siphonal canal of *O. pachyrhaphe* is relatively broader and the shell is more squamous. Its inclusion in *Orania* is based only on its shell morphology, which is close to *O. fusulus*, the type species of *Orania*.

Genus ***Pascula*** Dall, 1918
Type species by original designation: *Trophon citricus* Dall, 1908, Easter Island.
Evokesia Radwin & D'Attilio, 1972
Type species by original designation: *Sistrum rufonotatum* Carpenter, 1864.

Diagnosis. Shell with high spire, broadly elongate, ovate, nodose, not or rarely exceeding 20 mm in length at maturity. Axial sculpture of last teleoconch whorls consisting of moderately broad, high, rounded ribs. Spiral sculpture of moderately high and broad primary cords, narrow secondary cords and few threads.
Aperture ovate. Columellar lip weakly concave, smooth or with weak folds abapically, rim weakly erect abapically, adherent at small portion adapically. Outer lip with narrow, elongate denticles within.
Radula of the type species illustrated by Rehder [1980: 135, pl. 3 (3-4)] with three dimensional rachidian tooth bearing a long, narrow, projecting central cusp, a very small, narrow lateral denticle, a moderately long, moderately broad, lateral cusp and very weak marginal folds. No marginal cusp. Lateral teeth sickle shaped, with broad base.

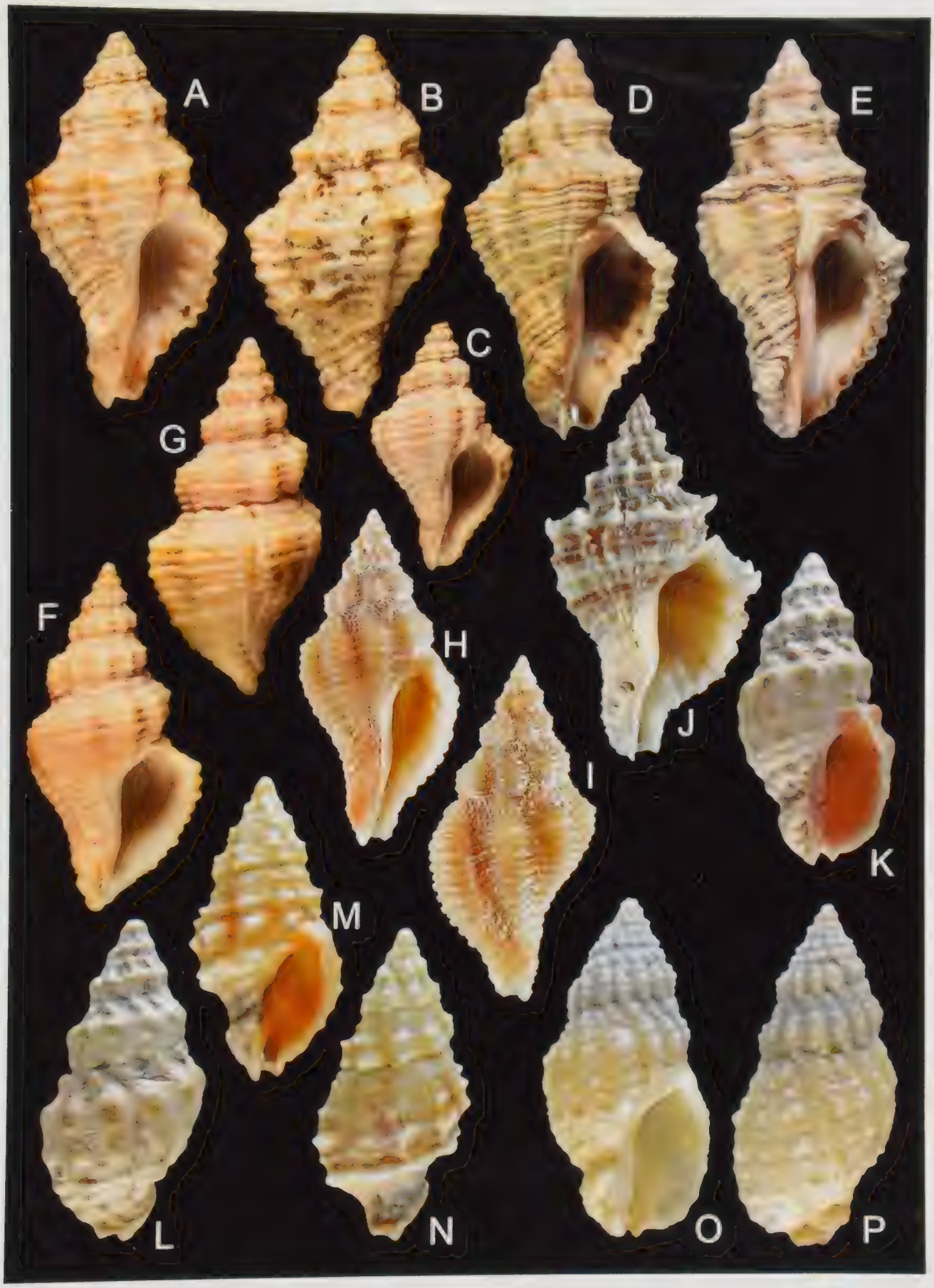
Remarks. Eight Recent species are assigned to *Pascula* in WoRMS (MolluscaBase 2018): *Pascula citrica* (Dall, 1908) (Easter Island and French Polynesia); *P. darrosensis* (E.A. Smith, 1884) (Indo-West Pacific); *P. muricata* (Reeve, 1846) (Indo-West Pacific); *P. ochrostoma* (Blainville, 1832) (Indo-West Pacific); *P. ozenneana* (Crosse, 1861) (Indo-West Pacific); *P. philpoppei* Houart, 2018 (Philippines and Japan); *P. rufonotata* (Carpenter, 1864) (Baja California, Mexico and Galapagos Islands); and *P. submissus* (E. A. Smith, 1903) (Indo-West Pacific).
One species, *P. palmeri* (Powell, 1967) (Fig. 22O-P) from New Zealand, is here added as a new combination. In the original description by Powell (1967: 193), *P. palmeri* was assigned to *Morula*. Although molecular genetic analyses are not yet available, the shell and radula morphology of *P. palmeri* (Figs 7G-H; 22O-P) is very close to *P. citrica* (Fig. 22K-L), the type species of *Pascula*. Thus, while waiting for a more complete genetic analysis of this genus, we suggest assigning *P. palmeri* to *Pascula* rather than to *Morula*, as the type species, *Morula uva* (Röding, 1798), is quite different from *P. palmeri*.

Genus *Tenguella* Arakawa, 1965
Type species by original designation: *Purpura granulata* Duclos, 1832, Indo-West Pacific.

Diagnosis. Shell with high spire, broadly ovate, nodose, rarely exceeding 30 mm in length at maturity. Axial sculpture of last teleoconch whorl consisting of 8-10 broad, rounded, nodose ribs. Spiral sculpture of strong, high, broad primary cords and numerous threads, forming relatively high nodes at intersection with axial ribs.
Aperture ovate. Columellar lip sinuous, smooth or with 1 or 2 narrow knobs abapically, rim very weakly erect abapically, otherwise adherent. Outer lip with strong denticles within.
Radula of the type species (Fig. 8C) with three dimensional rachidian tooth bearing a long, moderately broad, projecting central cusp, a very small, narrow lateral denticle, a moderately long, broad, lateral cusp and strong marginal folds giving rise to small, short marginal denticles, and a bifid marginal cusp. Lateral teeth sickle shaped, with broad base.

Figure 22

A-E. *Orania pachyrhaphe* (E.A. Smith, 1879)
A-B. Japan, Ukushima, Goto Islands, 33°15.5' N, 129°5' E, 11 fathoms (20 m), lectotype (here designated) NHMUK 1878.10.16.2/1, 20.9 mm; C. Paralectotype NHMUK 1878.10.16.2/2, 11 mm; D-E. Okinawa, Haneji Inland Sea, muddy areas on rocks, 0.3 – 1 m, RH (D. 26.4 mm; E. 23.7 mm).
F-I. *Bedevina birileffi* (Lischke, 1871)
F-G. Paralectotype of *Fusus pachyrhaphe* E.A. Smith, 1879, NHMUK 1878.11.7.28, 15.8 mm; H-I. Indonesia, near Belintung Is, Carima Straits, 15-20 m, RH, 14.8 mm.
J. *Lataxiena fimbriata* (Hinds, 1843), West Sumatra, RH, 23.7 mm.
K-L. *Pascula citrica* (Dall, 1908), Easter Id, Hanga Piko, RH, 13.8 mm.
M-N. *Pascula darrosensis* (E.A. Smith, 1884), Philippines, Sulu Sea, RH, 10.3 mm.
O-P. *Pascula palmeri* (Powell, 1967), New Zealand, Poor Knights Islands, on rock wall, 20 m, RH, 20.6 mm.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Remarks. The genus *Tenguella* currently includes five Recent species: *Tengualla ceylonica* (Dall, 1923), *T. granulata* (Duclos, 1832), *T. hoffmani* Houart, 2017, *T. marginalba* (Blainville, 1832) and *T. musiva* (Kiener, 1835). Two new species are described below giving a new total of 7 species in this genus (Table 2).

Tenguella granulata (Duclos, 1832)
Figs 8C; 23; 25Q-S

Purpura granulata Duclos, 1832: 111, pl.2, fig. 9.
Purpura tuberculata Blainville, 1832: 204, pl.9, fig. 3.
Purpura tuberculata var. *cingulifera* Kiener, 1835: pl.5, fig. 10[a].

Type material. *Purpura granulata*: not located (not in MNHN). The specimen illustrated by Duclos is here designated as lectotype (ICZN Art. 74.4). The original drawing is excellent (Fig. 23) and easily recognizable while the length given by Duclos (1 pouce = approximately 27 mm) fits perfectly for this species; *Purpura tuberculata*: 4 syntypes MNHN-IM-2000-777; *Purpura tuberculata* var. *cingulifera*: Not located in MHNG nor in MNHN.

Type localities. *Purpura granulata*: Australia ("Nouvelle-Hollande"); *Purpura tuberculata*: Red Sea and Madagascar, here restricted to the Red Sea; *Purpura tuberculata var. cingulifera*: unknown.

Distribution. *Tenguella granulata* is a very common species living throughout the Indo-West Pacific.

Remarks. *Tenguella granulata* is here compared with two species, *T. chinoi* n. sp. and *T. ericius* n. sp., collected during the MNHN/IRD expeditions in The Marquesas, Vanuatu and Papua New Guinea and known from a few other localities (see below).

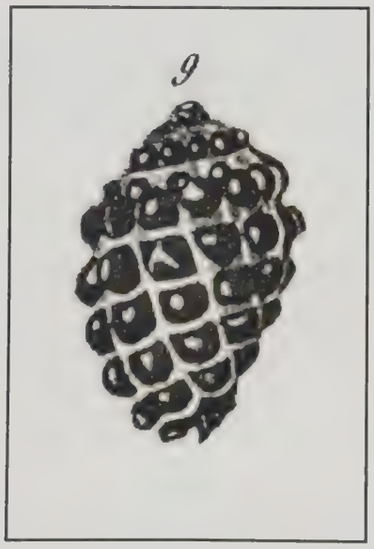

Fig. 23. *Purpura granulata*. Original illustration from Duclos, 1832.

Tenguella chinoi n. sp.
Figs 8A-B; 12A-B; 24; 25A-H

Morula mutica — Wilson, 1994: 44, pl. 5, figs 4 a-b [not *Azumamorula mutica* (Lamarck, 1816)].
Azumamorula sp. — Dharma, 2005: 168, pl. 59, figs 17a, b.
Morula (*Habromorula*) sp. — Tsuchiya, 2017: 958, pl. 251, fig. 1.

Type material. Holotype NHMUK 20080772/1 (reconstructed aperture and two pieces of tissue labelled "MORMUD.GM") (GenBank: FN677418), Guam, Mangalao, Pago Bay, near shore of eroded limestone cliffs, in open bay with near-shore fringing reef (syntopic with *T. ericius* n. sp).
Paratypes: **Guam**, Mangalao, Pago Bay, near shore of eroded limestone cliffs, in open bay with near-shore fringing reef, 3 lv, NHMUK 20080772/2 (fragments) (ex NHMUK 20080772).
Vanuatu, SANTO 2006, stn VM12, Palikulo Peninsula, 15°39'S, 167°16'E, 0-1 m, intertidal, soft bottom, 1 lv, MNHN-IM-2000-34214 (syntopic with *Tenguella granulata*); stn RAP15, North Tuvana Island, 15°37'S, 167°01'E, c. 2 m, 6 lv, 4 MNHN-IM-2000-34215; 2 RH (syntopic with *Tenguella granulata*); stn FM36, Vaucluse Passage, 15°22,4'S , 167°13'E, 0-1 m, intertidal, 1 lv, MNHN-IM-2000-34216 (syntopic with *Tenguella granulata* and *T. ericius* n. sp.).
Papua New Guinea, PAPUA NIUGINI, stn PM41, Wonad Island, 05°08'S, 145°49'E, sandy beach and intertidal rocks, 0-1 m, 6 lv, MNHN-IM-2000-34217 (syntopic with *Tenguella granulata* and *T. ericius* n. sp.);

Type locality. Guam, Mangalao, Pago Bay, near shore of eroded limestone cliffs, in open bay with near-shore fringing reef.

Other material examined. Papua New Guinea: PAPUA NIUGINI, stn PFM03, Bilbil Island, exposed steep, fringing reef, under rocks, exposed, 05°15'S, 145°47'E, 2 m, 2 lv (syntopic with *Tenguella granulata*); stn PM25, Barag Island, 05°01'S, 145°48'E, fringing reef, on narrow barrier island, 3 lv; stn PM33, Rempi area, bay on south side, coral reef, 05°02'S, 145°48'E, coral reef, 1 lv; stn PM43, Wonad Island, 05°08'S, 145°49'E, night tide, sandy beach and intertidal rocks, 0-1 m, 1 lv (syntopic with *Tenguella granulata*); stn PR76, Rempi area, SW Hargun Island, 05°02'S, 145°48'E, 2-15 m, 1 lv (syntopic with *Tenguella granulata*); stn PR192, Kranket Island, Cape Jantzen, 05°12'S, 145°49'E, 3-60 m, 2 lv; stn PR204, BilBil I., southern tip, no coordinates, 3-15 m, 2 lv (syntopic with *Tenguella granulata*); stn PR214, Tab Island, no coordinates, 1-8 m, 4 lv & 1 dd (syntopic with *Tenguella granulata* and *T. ericius* n. sp.); Hansa Bay, Madang Province, Laing Island, 2 lv, juv, (RH).

China Sea: (no other data), 11 lv (ex Staadt coll., 1969) (MNHN).
Western Australia: Exmouth, 1 lv (RH).

Distribution. Western Australia, Exmouth (1 RH), East Java (Dharma, 2005), Japan, Izu Islands and southwards (Tsuchiya, 2017), Papua New Guinea and Vanuatu; perhaps also the China Sea (MNHN). Intertidal to 3 m depth, sandy beach and intertidal rocks (Fig. 24).

Description. Shell small for the genus, up to 13.6 mm in length at maturity (paratype MNHN-IM-2000-34216) (Fig. 25B-C). Length/width ratio 1.3-1.4. Broad, heavy, nodose. Subsutural ramp broad, weakly sloping, concave.
Blackish-brown or black. Aperture white within with narrow black coloured narrow band at edge and dark bluish broad blotch at adapical part of strong curve of columellar lip.
Spire high, low. Teleoconch of up to 5 or 6 strongly convex, shouldered, nodose whorls. Suture adpressed. Protoconch and early teleoconch whorls strongly eroded in type material.
Axial sculpture of teleoconch whorls consisting of low, broad, nodose ribs with strong, low, broad nodes when crossing primary spiral cords. Last teleoconch whorl with 8 or 9 low, occasionally indistinct ribs, eroded on earlier whorls. Spiral sculpture of low, strong, rounded and flat, broad, nodose, primary cords and low, narrow threads. Last teleoconch whorl with SP, P1-P5 with 2-4 flat, narrow, smooth threads between each pair of cords. SP very broad, obvious, usually broader than other spiral cords. P1-P2 similar in size, P3-P5 decreasing in strength abapically. P5 very narrow.
Aperture large, very narrow, strongly ovate, sinuous. Columellar lip broad, strongly curved, with one or two very narrow knobs abapically and low parietal tooth at adapical extremity. Rim weakly partially erect abapically, adherent adapically. Anal notch narrow, moderately deep. Outer lip weakly erect, smooth, edge broad with 4 strong, high denticles within, consisting of D1-D4. D1 very broad and high, D2 more than half the size of D1, D3 and D4 lower and narrower, more elongate within aperture. Siphonal canal very short, 9-10% of total shell length, narrow, straight, broadly open.
Radula consisting of a rachidian with a moderately large, long, central cusp, a short, narrow, lateral denticle and a moderately broad, long, lateral cusp on each side, 2 or 3 obvious, short, marginal denticles and a short marginal cusp. Lateral teeth sickle shaped with broad base and narrow extremity.

Remarks. Based on molecular data, *Tenguella chinoi* n. sp. was separated from *Tenguella granulata*, *T. ceylonica*, *T. musiva* and *T. marginalba* by Claremont et al (2013, as "*Tenguella* n. sp."). These five species formed a well-supported subclade. We here confirm this result (Fig 3).
The material studied in Claremont et al. (2013) (as *Tenguella* n. sp.) consists of six specimens, four of them were crashed to obtain the soft parts, two remained intact, one of those is here illustrated (Fig. 25P). These two intact specimens are obviously what is here described as *T. ericius* n. sp. and so, the NHMUK material was first identified as this species.
However, in the meantime, two specimens of *T. ericius* n. sp. from the PAKAIHI I TE MOANA expedition in the Marquesas Archipelago were also analyzed in MNHN and proved to be different with around 10% of genetic distance (COI gene) from the specimen analyzed in Claremont et al. (2013).
This unexpected result could mean two things: either the Marquesas species is a sibling species but is genetically different, or the material in Claremont et al. (2013) was composed of different species and the specimen analyzed by these authors was not *T. ericius* n. sp. After a very careful examination of the crushed shells, the reconstruction of the aperture of one studied specimen was possible (Fig. 25A) and it is clearly this second hypothesis which is the correct one. The species studied in Claremont et al. (2013) is clearly the species described here as *T. chinoi* n. sp. while the two intact, not studied specimens are undoubtedly *T. ericius* n. sp.
These two species, *T. ericius* n. sp. and *T. chinoi* n. sp. are syntopic in some localities and thus also in Guam, where the specimens analyzed in Claremont et al. (2013) were collected. Thanks now to the results obtained by the analysis of *T. ericius* n. sp. from the Marquesas it is also proved that the two species are genetically different. For other differences between these two species see under *T. ericius* n. sp.
The protoconch and the first teleoconch whorls were preserved in two juvenile specimens from Papua New Guinea (RH). The protoconch is conical and glossy brown, consisting of 3.5 whorls and a terminal lip of the sinusigera type (Fig. 25G). Some specimens collected in the China Sea (no other locality data) before 1960 and deposited in MNHN are bigger and reach a length of 16 mm (Fig. 25H).
The shell morphology of this little species confirms its separation from the other *Tenguella* species and, more particularly, from the similar looking *T. granulata*.
Tenguella granulata is a species with a quite variable shell morphology (Fig. 25Q-S), but it differs consistently from *T. chinoi* n. sp. in being less stocky, with more acute nodes, in having a comparatively larger shell, often reaching a length of more than 25 mm, with an average size of 15-20 mm, compared to the 12-16 mm of *T. chinoi*. The spire in *T. granulata* is higher and more acute; the aperture is larger, broader, and less sinuous, with relatively smaller, less obvious denticles and a narrower outer apertural lip.
Tenguella chinoi n. sp. was illustrated by Dharma (2005) as *Azumamorula* sp. This monotypic genus still needs to be analysed carefully, but *A. mutica*

(Lamarck, 1816), the type species of *Azumamorula* (Fig. 27A-B), differs consistently from *Tenguella* in having a broadly convex, smoother shell with obsolete axial ribs and very low spiral sculpture. It also has a broader aperture with comparatively weaker denticles.

Etymology. Named after Mitsuo Chino (Japan), known for his numerous contributions to malacology and author of several new species, who sent me some of the shells included in the studies of Ergalataxinae.

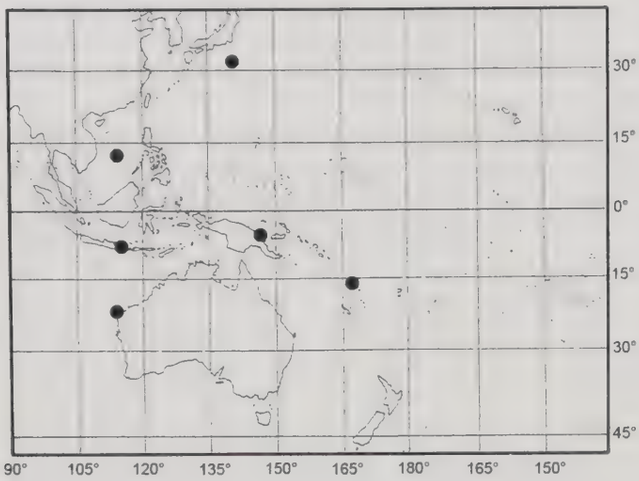

Figure 24. Distribution of *Tenguella chinoi* n. sp.

***Tenguella ericius* n. sp.**
Figs 12C-D; 25I-P; 26

Morula granulata — Wells et al., 1990: 44, pl. 21, fig. 141 (not *Tenguella granulata*).

Type material. holotype MNHN-IM-2013-67609 (BOLD MUBA788-18; GenBank MK216559), Marquesas, PAKAIHI I TE MOANA, stn MQ7-M, Baie des Controleurs, 8°54'S, 140°03'W, intertidal.

Paratypes: **Marquesas:** PAKAIHI I TE MOANA, stn MQ7-M, Baie des Controleurs, 8°54'S, 140°03'W, intertidal, 1 lv, MNHN-IM-2013-67608 (BOLD MUBA787-18; GenBank MK216547).
Vanuatu: SANTO 2006, stn VM06, Vanuatu, Maloka Island, 15°35 S, 166°59'E, intertidal, rock bottom, 1 lv (paratype MNHN-IM-2007-18187); stn FM36, Vaucluse Passage, 15°22,4'S , 167°13'E, 0-1 m, intertidal, 3 lv, MNHN-IM-2000-34218 (Fig. 25N-O) (syntopic with *Tenguella granulata* and *T. chinoi* n. sp.).
Papua New Guinea: PAPUA NIUGINI, stn PM41, Wonad Island, 05°08'S, 145°49'E, sandy beach and intertidal rocks, 0-1 m, 14 lv (13 MNHN-IM-2000-34219, 1 RH) (syntopic with *Tenguella granulata* and *T. chinoi* n. sp.); stn PR214, Tab Island, 05°15'S, 145°47'E, 1-8 m, 1 dd, MNHN-IM-2000-34220 (syntopic with *Tenguella granulata* and *T. chinoi* n. sp.).
Guam: Mangalao, Pago Bay, near shore of eroded limestone cliffs, in open bay with near-shore fringing reef, 2 lv, NHMUK 20180544 (ex NHMUK 20080772) (syntopic with *T. chinoi* n. sp.) (see under that species).

Type locality. Marquesas, Pakaihi I Te Moana, stn MQ7-M, Baie des Controleurs, 8°54'S, 140°03'W, intertidal.

Other material examined. Marquesas: Taiohae, Nuku Hiva Island, 1 lv, 1 dd (RH).
China Sea: (no other data), 9 lv, 2 dd (ex Staadt coll., 1969) (MNHN).

Distribution. China Sea (no other data), Christmas Island (Indian Ocean) (Wells et al. 1990), Guam, Papua New Guinea, Vanuatu and Marquesas (Fig. 26).

Figure 25 (scale bar: 500 μm)

A-H. *Tenguella chinoi* n. sp.
A. Guam, Mangalao, Pago Bay, near shore of eroded limestone cliffs, in open bay with near-shore fringing reef, holotype NHMUK 20080772/1, GenBank: FN677418, reconstructed aperture, 10 mm; B-C. Vanuatu, SANTO, stn FM36, 15°22,4'S, 167°13'E, 0-1 m, paratype MNHN-IM-2000-34216, 13.6 mm; D-F. Papua New Guinea, Papua Niugini, stn PM41, 05°08,1'S, 145°49, 0-1 m, paratype MNHN-IM-2000-34217, 12.1 mm; G. Protoconch, Papua New Guinea, Hansa Bay, Laing Island, RH; H. China Sea (no other data), MNHN, 15.3 mm.
I-P. *Tenguella ericius* n. sp.
I-J. Marquesas, Pakaihi I Te Moana, stn MQ7-M, Baie des Controleurs, 8°54' S, 140°03' W, intertidal, holotype MNHN-IM-2013-67609, (BOLD MUBA788-18; GenBank MK216559), 13.1 mm; K-M. Vanuatu, SANTO stn VM06, Vanuatu, Maloka Id,15°35', 166°59' E, intertidal, paratype MNHN IM-2007-18187, 13.9 mm; N-O. Vanuatu, SANTO, stn FM36, 15°22,4'S, 167°13'E, 0-1 m, paratype MNHN-IM-2000-34218, 13.9 mm; P. Guam, Mangalao, Pago Bay, near shore of eroded limestone cliffs, in open bay with near-shore fringing reef, paratype NHMUK 20180544 (ex NHMUK 20080772), 14.8 mm.
Q-S. *Tenguella granulata* (Duclos, 1832)
Q-R. Papua New Guinea, Papua Niugini, stn PR214, 08/12/2012, 1-8 m (no other information), MNHN, 17.2 mm; S. Vanuatu, SANTO, stn RAP15,15°36,6'S, 167°01'E, 2 m, MNHN, 19.9 mm.

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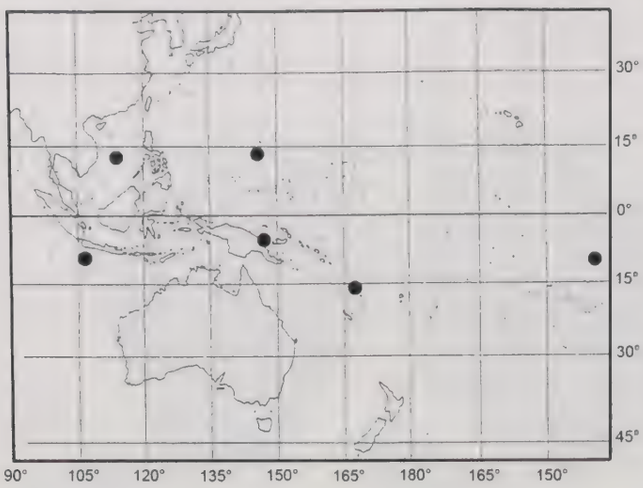


Figure 26. Distribution of *Tenguella ericius* n. sp.

Description. Shell small for the genus, up to 15.3 mm in length at maturity. Length/width ratio 1.4-1.5. Biconical, broad, heavy, weakly spinose and nodose, tuberculate. Subsutural ramp strongly sloping, concave.

Blackish-brown or black. Aperture white within with narrow black coloured narrow band at edge and dark bluish broad blotch at adapical weak curve of columellar lip.

Spire moderately high. Teleoconch of up to 5 broad, shouldered, nodose whorls. Suture adpressed. Protoconch eroded in all specimens.

Axial sculpture of teleoconch whorls consisting of narrow, moderately high, nodose ribs. Early spire whorls with 12 or 13 ribs; last whorl with 9 ribs with strong, relatively high, broad nodes at intersection with primary spiral cords. Nodes higher and more apparent on apertural rib. Spiral sculpture of low, strong, rounded, broad, nodose, primary cords with 2 or 3 very narrow, rounded threads between each pair of cords. Last teleoconch whorl with broad SP, similar to P1-P3, P4 narrower, P5 narrowest primary cord.

Aperture large, ovate. Columellar lip broad, smooth or with one or two very small denticles abapically and low parietal tooth at adapical extremity. Anal notch moderately deep, broad, with an open channel shortly extending in SP spine. Outer lip weakly erect, smooth, with 4 strong, broad denticles within consisting of D1-D4; D1 broadest and strongest, D2-D4 decreasing in strength abapically. Siphonal canal very short, 3.5-5.5% of total shell length, narrow, straight, broadly open.

Operculum and radula unknown.

Remarks. *Tenguella chinoi* n. sp. differs consistently from *T. ericius* in having a slightly broader, more globose, stocky and solid shell, with broader and lower axial ribs; and in having blunt, broad nodes compared to the more spiny shell of *T. ericius* n. sp. *T. chinoi* also has a more sinuous columellar lip and broader, more apparent apertural denticles within the outer lip, resulting in a much more narrower aperture as opposed to a relatively broad aperture in *T. ericius* n. sp. In *T. chinoi* the spire is also lower and less acute, the outer apertural lip is relatively broader, and the siphonal canal, although short in *T. chinoi* n. sp., is comparatively longer (9-10% of the total shell length) than in *T. ericius* (3.5-5.5 % of the shell length).

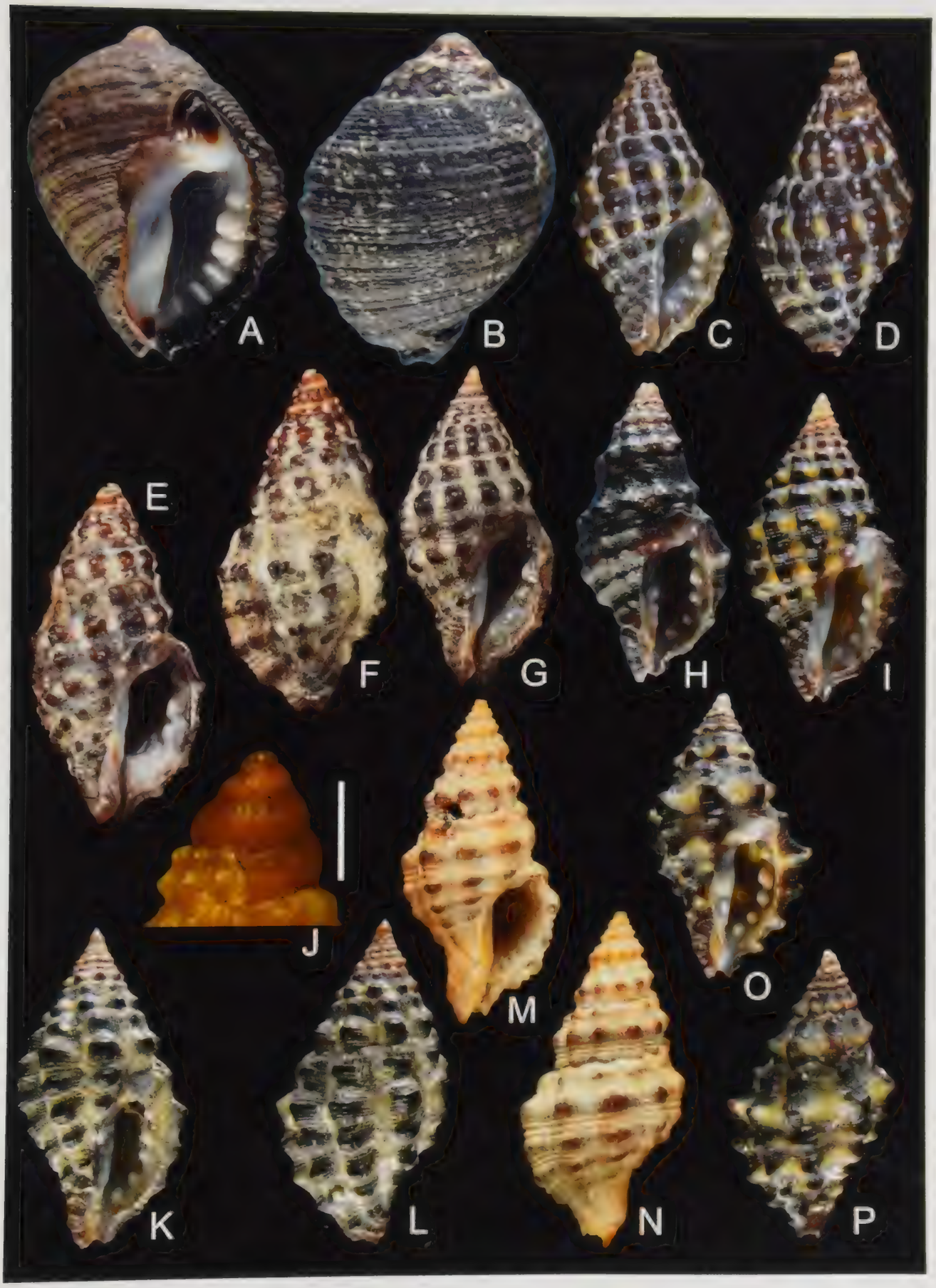
Tenguella granulata differs from *T. ericius* n. sp. in having an obviously larger shell and a comparatively narrower aperture due to a strongly folded columellar lip. The outer apertural lip of *T. granulata* is almost similar than that of *T. ericius* n. sp., but it is obviously less expanded abaperturally at the level of P4, between D3 and D4 (Fig. 12D).

Etymology. *Ericius*: hedgehog, named after its spinose shell.

Discussion. *Tenguella granulata*, *T. chinoi* n. sp. and *T. ericius* n. sp. are syntopic in PAPUA NIUGINI, stn PM41 and PR214, and in SANTO 2006, stn FM36; *T. chinoi* n. sp. and *T. ericius* are also syntopic in Guam (see under *T. chinoi* n. sp.). *Tenguella granulata* and *T. chinoi* n. sp. are syntopic in PAPUA NIUGINI stn PFM03, PM43, PR76 and PR204, and in SANTO stn VM12 and RAP15.

Figure 27 (scale bar: 500 μm)

A-B. *Azumamorula mutica* (Lamarck, 1816), Reunion Id, harbour, 2-3 m, RH, 18.2 mm.
C-L. *Claremontiella nodulosa* (C.B. Adams, 1845)
C-D. Jamaica, lectotype MCZ 177045, 14.9 mm (photo Jennifer Trimble, curatorial assistant, MCZ); E-G. Syntypes of *Ricinula ferruginosa* Reeve, 1846, "W. Indies added to board", H. Cuming collection, NHMUK 1968462. E-F. 18.9 mm; G. 17.3 mm (photo Harry Taylor, NHMUK Photographic Unit, © Natural History Museum of London); H. Cape Verde, Sal Id, RH, 14.6 mm; I. Tobago, Rocky Point, Mt Irvine Bay, RH, 15.4 mm; J. Protoconch, Cuba, RH; K-L. West Africa, Angola, Cape Esterias, RH, 15.2 mm.
M-P. *Claremontiella consanguinea* (E.A. Smith, 1891)
M-N. St. Helena, lectotype NHMUK 1889.10.1.2368, 17.4 mm (photo Harry Taylor, NHMUK Photographic Unit, © Natural History Museum of London); O-P. Sao Tome, Praia Emilia, RH, 13.8 mm.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Tenguella ericius n. sp. was also collected in the China Sea prior to 1960, where it is probably sympatric with *T. granulata* and *T. chinoi* n. sp., but specific locality data is missing (MNHN). As for *T. chinoi* n. sp., the specimens of *T. ericius* n. sp. collected in the China Sea are larger, reaching a length of 17.5 mm.

Another shell, misidentified as *M. granulata*, was illustrated by Wells et al. (1990). It is undoubtedly *T. ericius*. The localities given (Christmas Island and Cocos/Keelings Islands, Indian Ocean) are not unexpected, but the stated size of the shell (2 cm) is far larger than the other known specimens.

Claremontiella new genus

Figs 8D-F; 11G; 27C-P; 28A-E

Type species: *Purpura nodulosa* C.B. Adams, 1845: 2, eastern and western Atlantic (Fig. 27C-L).

Other included species. *Claremontiella adiakritos* n. sp. and *C. consanguinea* (E.A. Smith, 1891) (new combination).

Description. Shell moderately broad with high spire and 7 or 8 rounded, nodose axial ribs, crossed by a subsutural spiral cord and 5 primary spiral cords on convex part of teleoconch whorl, with additional, low, narrow, secondary and tertiary cords. Protoconch conical with 3.5 whorls and sinusigeral terminal notch.

Aperture narrow, ovate. Columellar lip smooth or with low denticles abapically and low parietal tooth at adapical extremity, weakly concave, rim adherent to shell. Anal notch broad, moderately deep. Outer apertural lip smooth with low denticles within. Siphonal canal short, 12-14% of total shell length, narrow, open.

Radula of *Claremontiella* of three-dimensional type consisting of a rachidian bearing a narrow, long, central cusp, a narrow, very short, lateral denticle on each side, a broad, short lateral cusp, a few marginal folds and a short marginal cusp. Lateral teeth sickle shaped, narrow with a slightly broader base (Fig. 8D-F).

Distribution. Eastern and western South Atlantic, Eastern Pacific, Gulf of California and Baja California, Mexico.

Remarks. Houart (1997: 64) considered *Claremontiella consanguinea* (E. A. Smith, 1891) (Figs 8E-F; 27M-P) a valid species and assigned it to *Morula*, together with *C. nodulosa*. The shell of *C. consanguinea* was separated from *C. nodulosa* by having a narrower shell with lower nodes, more broadly spaced spiral cords, a relatively longer siphonal canal and a less denticulate or smooth aperture. Since then, we have had the opportunity to examine more specimens of *Claremontiella* species from off West Africa, especially a population living in São Tomé (Fig. 27O-P). In these specimens, the shell looks strongly similar to the original illustration of *Cantharus consanguineus*.

Having sent typical specimens of *C. nodulosa* from Virgin Islands, close to Jamaica, the type locality of *C. nodulosa* and a species identified as *C. consanguinea* from São Tomé for genetic analyses, we received an opinion from Andrea Barco (in litt, 17 June 2013) who said, "There is little genetic distance between the two groups, but it is really low. I would expect higher values between different species."

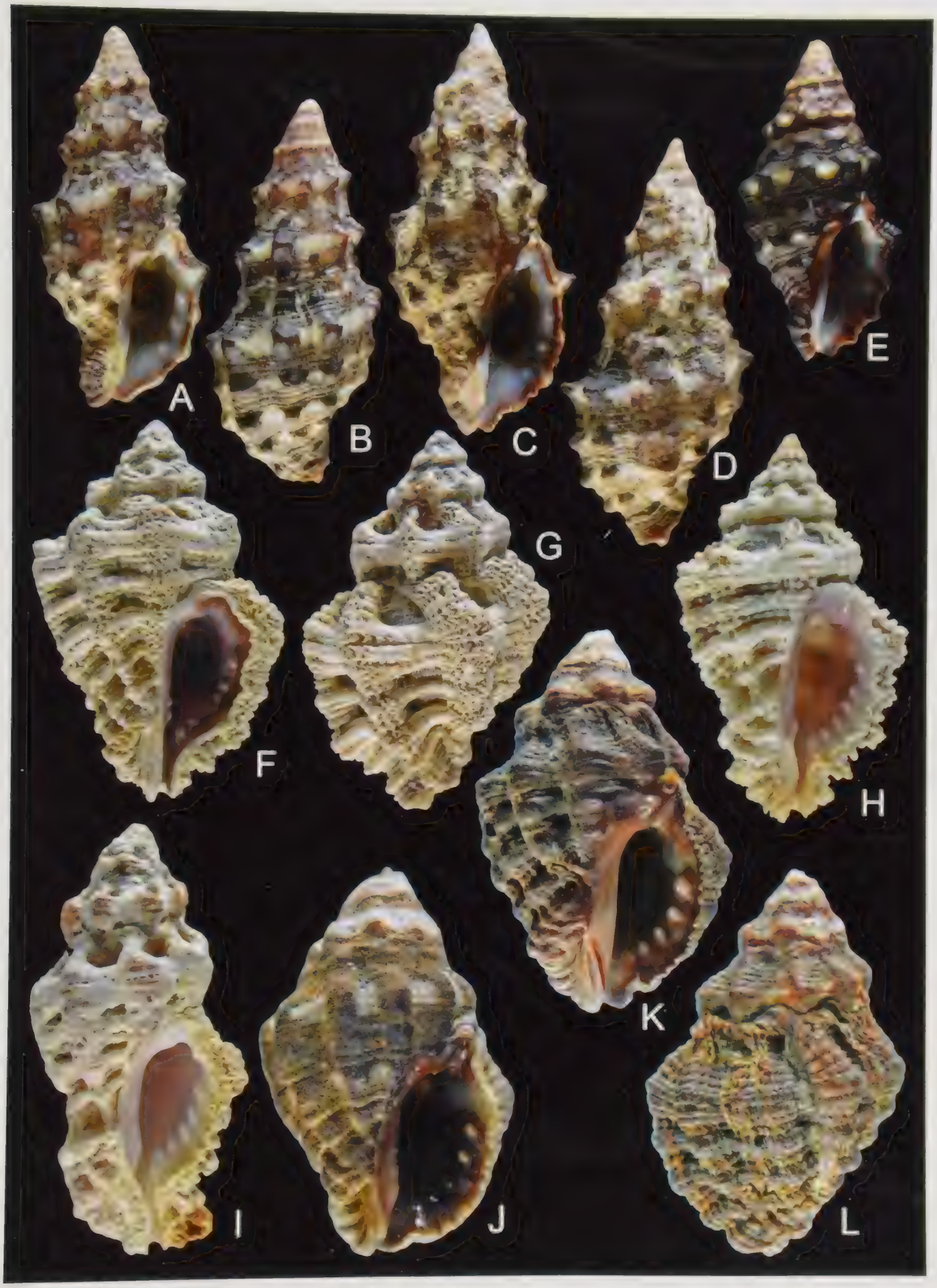
There is little doubt that some genetic differences could exist between populations from São Tomé and Saint Helena, so the names *Claremontiella consanguinea* and *C. nodulosa* could be subjective synonyms. Further analyses are needed before making a final decision. In the meantime *C. consanguinea* is here provisionally retained as a valid species.

Claremontiella adiakritos n. sp. is assigned to *Claremontiella* because of its similar shell and radula morphology. The shell of *C. adiakritos* is close to the type species (Figs 27H and 28E) with which it has often been confused, as *Morula*, *Evokesia*, or *Pascula ferruginosa* (see under *C. adiakritos* n. sp.).

Etymology. The new genus is named for Martine Claremont whose contribution to the molecular phylogeny of Muricidae, in particular here for the Ergalataxinae, while working at the Natural History Museum, London, was extremely useful and appreciated.

Figure 28

A-E. *Claremontiella adiakritos* n. sp.
A-D. West Mexico, Mazatlan. A-B. Holotype NHMUK 20180545, 23.3 mm; C-D. Paratype RH, 24.7 mm; E. West Mexico, Baja California, near San Felipe, Alecia Playa, RH, 15.2 mm.
F-H. *Murichorda fiscellum* (Gmelin, 1791)
F-G. South of west Java, Sancang, low tide, under rocks, RH, 23.2 mm; H. Aden, Gulf of Aden, RH, 26.2 mm.
I. *Murichorda jacobsini* (Emerson & D'Attilio, 1985), Solomon Islands, Guadalcanal, Marau Sound, RH, 37.3 mm.
J-L. *Murichorda rumphiusi* (Houart, 1996).
J. Ambon, Hito, east side of Laha, paratype RH, 19.7 mm; K-L. Singapore, east coast of Park Beach, intertidally, muddy rocks, RH, 19.6 mm.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***Claremontiella adiakritos* n. sp.**
Figs 8D; 11G; 28A-E; 30

Morula ferruginosa — Keen, 1958: 376, sp. 411; Abbott, 1974: 178, fig. 1875 (not *Ricinula ferruginosa* Reeve, 1846).
Morula (*Morunella*) *ferruginosa* — Keen, 1971: 554, fig. 1092; Victor Alamo & Violeta Valdivieso, 1997: 54 (not *Ricinula ferruginosa* Reeve, 1846).
Evokesia ferruginosa — Radwin & D'Attilio, 1972: 338, fig. 1A; Radwin & D'Attilio, 1976: 143, pl. 3, fig. 5; Kaicher, 1979, card 2038 (not *Ricinula ferruginosa* Reeve, 1846).
Pascula ferruginosa — Vokes, 1984: 2014, 215 (not *Ricinula ferruginosa* Reeve, 1846).
Morula (*Morula*) *ferruginosa* — Skoglund, 2002: 116 (not *Ricinula ferruginosa* Reeve, 1846).

Type material. Holotype NHMUK 20180545, West Mexico, Mazatlan, lv.
Paratypes: West Mexico, Mazatlan, lv, 2 RH; Mexico, Baja California Sur, Playa Santispac, about 30 km south of Mulege, 2 IRSNB I.G. 33893; MT. 3744, 2 MNHN-IM-2000-34221
.

Type locality. West Mexico, Mazatlan.

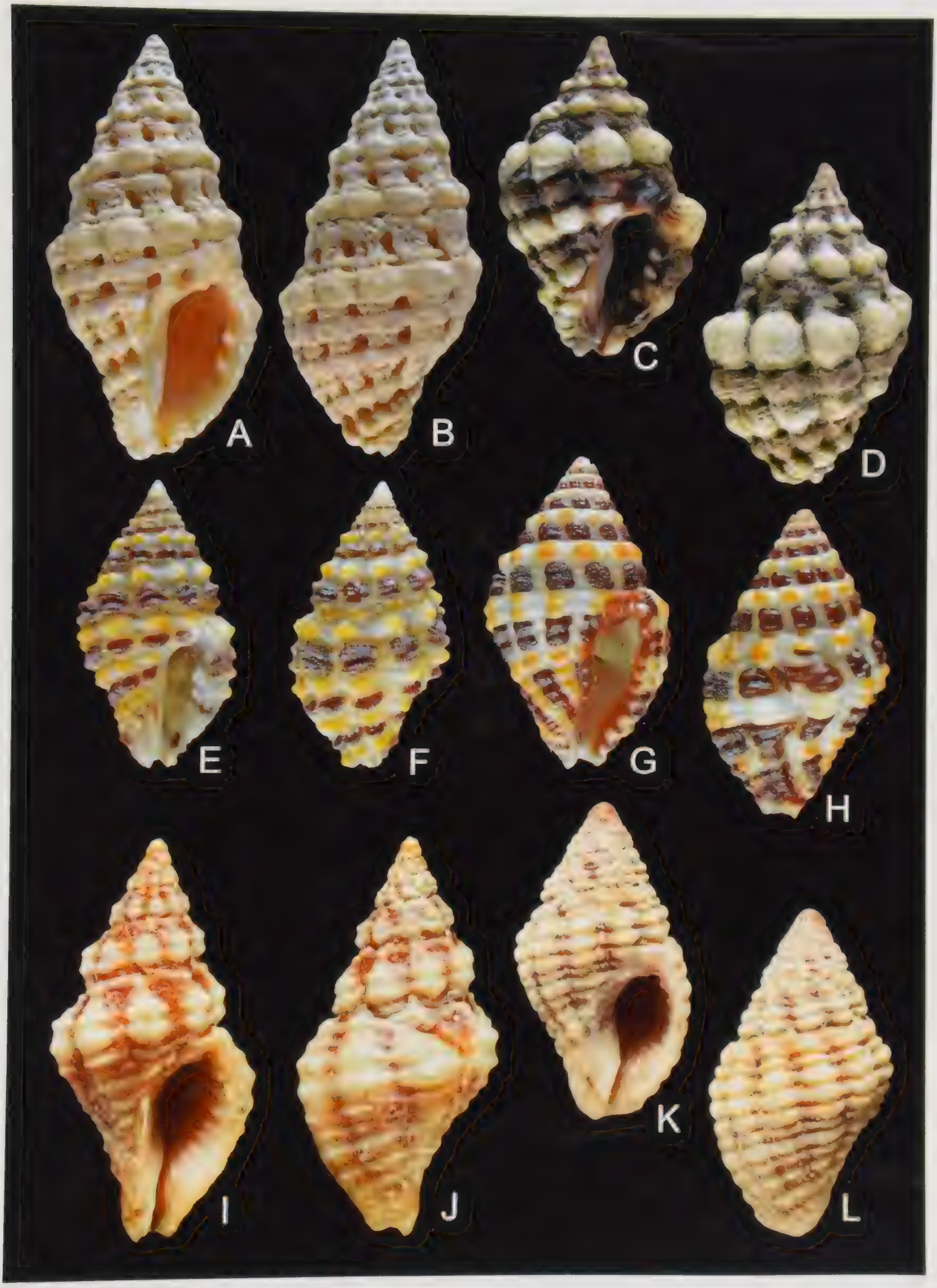
Other Material examined. Baja California, Mexico, Alecia Playa, near San Felipe, 24 lv & dd, RH; Guaymas, 3 lv & dd, RH (radula illustrated); Mexico, Adair Bay, 2 lv, RH; Gulf of California (no other data), 3 lv, RH; Mexico, Mulege, 2 dd, RH; Baja California, Mexico, Puertocitos, 1 dd, RH; Baja California, Mexico, La Paz, 2 lv, RH.

Distribution. Magdalena Bay, Baja California, through the Gulf of California and south along the Sonoran coast of Mexico at least as far as Guaymas, intertidally, under rocks (Keen, 1971). Its distribution south to Bocapán, El Rubio and Tumbes, Peru (Alamo & Valdivieso, 1987, 1997 and Skoglund, 2002) is doubtful (see remarks). Finet (1994: 50) mentions records from the Galapagos Islands but without any illustration, which is also here considered doubtful (Fig. 30).

Description. Shell large for the genus, up to 24.7 mm in length at maturity (paratype RH). Length/width ratio 2.1-2.3. Lanceolate, narrow, heavy, nodose. Subsutural ramp broad, strongly sloping, concave.
Dark brown or blackish-brown, white between nodes of first primary cord (P1), also on other cords but less obvious. Aperture bluish-white within with brown band within outer lip up to white apertural denticles. Columellar lip bluish-white with a darker area abapically.
Spire very high with teleoconch up to 6 weakly convex, narrow, angulate, shouldered, nodose whorls. Suture adpressed. Protoconch in examined material unknown, eroded in all specimens.
Axial sculpture of teleoconch whorls consisting of low, weak, narrow, rounded ribs with moderately high, sharp nodes at intersection of primary spiral cords. First and second whorls eroded in all specimens, third whorl with 10 ribs, fourth with 9, fifth with 9 or 10, last whorl with 7 ribs. Spiral sculpture of low, rounded, broad, nodose primary cords and numerous threads. Last teleoconch whorl with SP, P1-P5 and additional threads between each pair of cords. P1 broadest, P2-P3 weakly narrower, similar in strength, P4 narrower and lower, P5 smallest on adapical part of siphonal canal.
Aperture small, ovate. Columellar lip narrow, smooth, rim adherent, with very weak low parietal tooth at adapical extremity. Anal notch shallow, broad. Outer lip smooth with low, small denticles within, consisting of D1-D4, strongly decreasing in strength abapically; very low ID occasionally observed. Denticles sometimes obsolete. Siphonal canal very short, 10-12% of total shell length, narrow, weakly dorsally recurved, broadly open.
Operculum dark brown, ovate with subapical nucleus in lower right.
Radula of three-dimensional type consisting of a rachidian bearing a narrow, long, central cusp, a narrow, very short, lateral denticle on each side, a broad, shorter lateral cusp and few marginal folds. Lateral teeth sickle shaped, narrow with a slightly broader base.

Figure 29

A-B. *Muricodrupa fenestrata* (Blainville, 1832), New Caledonia, Ouvea, RH, 30.3 mm.
C-D. *Muricodrupa anaxares* (Kiener, 1835), South Africa, Durban, Reunion rocks, low tide, in rock crevices, RH, 14.6 mm.
E-F. *Lauta parva* (Reeve, 1845), Philippines, Cebu, RH, 9.4 mm.
G-H. *Engina alveolata* (Kiener, 1836), Fiji, Wayasawa group, Wasayama Id, under coral slab, low tide, RH, 12.9 mm.
I-L. *Cantharus* (*Tritonidea*) *albozonatus* Smith, 1890, St. Helena, W.H. Turton collection.
I-J. Syntype NHMUK 1889.10.1.2356-2361, 15.8 mm; K-L. Syntype NHMUK 1889.10.1.152-161, 10.9 mm.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Remarks. Vokes (1984) figured Reeve's illustrated syntype of *Ricinula ferruginosa* (NHMUK 1968462) and noted that the syntypes were specimens of the Atlantic *Trachypollia nodulosa* (C.B. Adams), leaving the Pacific species without a name. Vokes (1984) also illustrated the lectotype of *T. nodulosa*.

Claremontiella adiakritos n. sp. is assigned to *Claremontiella* because the shell and radula morphology are similar to those of *C. nodulosa*, type species of the genus, and to *C. consanguinea*.

The species has a very high spire with a low subsutural spiral cord; low, narrow cords on subsutural ramp; five low, broad, spiral cords on convex part of teleoconch whorl; numerous spiral threads; and a very short siphonal canal. The outer apertural lip bears low denticles within, and is occasionally smooth.

The ontogeny of the spiral cords is unknown since all examined specimens were badly corroded from the first to the second or third teleoconch whorls. For this reason, the protoconch could also not be examined. However, Radwin & D'Attilio (1972: 338) described and illustrated the protoconch of *C. adiakritos* n. sp. (as *Evokesia ferruginosa*) with 3.5 papillose whorls, similar to the protoconch morphology of the type species of *Claremontiella* (Fig. 27J).

The radula of this species, illustrated in Radwin & D'Attilio (1972: 340, fig. 16), is strangely different from that illustrated here (Fig. 8D), extracted from a specimen collected near San Felipe. The drawing shows a broader and shorter central cusp, and broader lateral cusps as well as broad lateral teeth, while the SEM here illustrated shows a typical ergalataxine radula, very close to that of *C. consanguinea*, with a narrow, long central cusp, a very short lateral denticle on each side, short, moderately broad lateral cusps and narrow, slender, lateral teeth.

The assignation of this species to *Claremontiella* n. gen. is tentative and requires genetic analyses for confirmation.

Alamo & Valdivieso (1987, 1997) reported this species (without any figure) from Bocapán and El Rubio, Tumbes, Peru, but *Claremontiella adiakritos* n. sp. has been frequently confused with *Trachypollia lugubris* and no voucher material was referenced (V. Mogollon, in litt.). Therefore, the presence of *C. adiakritos* in Peru and the Galapagos Islands remains doubtful.

Claremontiella nodulosa differs from *C. adiakritos* n. sp. in having a shell with slightly larger primary spiral cords with rounded nodes instead of more sharp knobs, and in having a generally less high spire, a broader, obvious and nodose subsutural cord, and a darker coloured aperture with thicker outer apertural lip and more obvious denticles within.

Etymology. *Adiakritos* (G) meaning mixed, undistinguishable, named for its resemblance to some forms of *Claremontiella nodulosa* (C.B. Adams, 1845), with which it has often been confused in literature.

Figure 30. Distribution of *Claremontiella adiakritos* n. sp.

Murichorda new genus
Figs 8G-H; 9A; 28F-L

Type species: *Purpura fiscellum* Gmelin, 1791: 3552, Indo-West Pacific.

Other included species. *Murichorda rumphiusi* (Houart, 1996) (new combination) and *Murichorda jacobsini* (Emerson & D'Attilio, 1985) (new combination).

Description. Shell large, up to 44.5 mm in length, broadly ovate, weakly angulate, shouldered, with 6-8 broad, high, rounded axial ribs, crossed by 5 high, longitudinally grooved primary spiral cords, occasionally deeply excavated between each pair of cords. Intersection of axial ribs and primary spiral cords forming low, broad knobs. Aperture broadly ovate with low denticles within outer lip. Siphonal canal short to moderate in length, 13-29% of total shell length, broadly open.

Radula ergalataxine (Figs 8G-H; 9A), of three-dimensional type, consisting of a narrow, long central cusp, a very short, narrow, lateral denticle on each side, a broad, moderately long lateral cusp and occasionally a few low marginal folds. Lateral teeth sickle shaped, broad.

Distribution. Throughout the Indo-Pacific.

Remarks. *Murichorda fiscellum* was previously assigned to *Cronia* H. & A. Adams, 1853 by Cernohorsky (1969: 311; 1982: 113), but *Cronia*, type species *C. amygdala* (Kiener, 1835), was included in a different clade by Claremont et al. (2013), together

with *Ergalatax* Iredale, 1931 and *Maculotriton* Dall, 1904, which could be potential synonyms (see Table 2).

Because its shell morphology is close to *M. fenestrata* (Blainville, 1832), the type species of *Muricodrupa*, *Murichorda fiscellum* has been assigned to *Muricodrupa* by numerous authors, starting with Kay (1979). However, in Claremont et al. (2013) "*Morula*" *fiscella* and "*Morula*" *rumphiusi* formed a well-supported clade in all analyses but were excluded from *Muricodrupa*. Both are therefore here assigned to *Murichorda* new genus, along with *Murichorda jacobsini*.

Etymology. Prefix *Muri*, from Muricidae + suffix *chorda* (L): rope, twine. Named for the strong, broad spiral cords, a characteristic shared by the shells assigned to this new genus.

Lauta new genus
Fig. 29E-F

Type species: *Ricinula parva* Reeve, 1846: pl. 6, fig. 43.

Description. Shell small, up to 10 mm in length, weakly ovate and shouldered, nodose, with 7 or 8 axial ribs crossed by narrow, rounded, primary cords consisting of SP near suture, P1-P5 on convex part of teleoconch whorl and ADP on siphonal canal, with rounded, high nodes at intersection of axial ribs and spiral cords.

Spire high with conical protoconch of 3.5 whorls. Aperture strongly ovate, narrow, with strong denticles within outer lip. Columellar lip narrow, almost straight, smooth, rim almost entirely adherent to shell. Anal notch broad, moderately deep. Siphonal canal short, 10-13% of total shell length. Radula unknown.

Distribution. Philippine Islands.

Remarks. *Lauta parva* is sister to all other members of subclade Z in Claremont et al (2013: fig. 1-3B), suggesting that a new genus is required for this species. The genus *Morula* Schumacher, 1817 in which *Lauta parva* was previously included consisted of 19 species. One of them, *M. anaxares*, is now assigned to *Muricodrupa* Iredale, 1918; two species, *M. nodulosa* and *C. consanguinea*, are now assigned to *Claremontiella* n. gen.; one species, *M. rumphiusi*, is now assigned to *Murichorda* n. gen.; and one species, *M. parva*, is here assigned to *Lauta* n. gen. Of the 14 remaining species of *Morula* s.s., six were analysed by Claremont et al (2013): *M. aspera* (Lamarck, 1816), *M. chrysostoma* (Deshayes, 1844), *M. echinata* (Reeve, 1846) (= *Sistrum ventricosulum* G. & H. Nevill, 1875, new synonymy) (as *M. benedicta* in Claremont et al., 2013), *M. nodicostata* (Pease, 1868), *M. uva* (Röding, 1798) and *M. zebrina* Houart, 2004. The eight remaining species are here provisionally retained in *Morula* s.s. (Table 2), pending future genetic analyses.

Etymology. The generic name *Lauta* (L: neat, elegant) is derived from *Ricinula lauta* Reeve, 1846, junior synonym of *Engina alveolata* (Kiener, 1836) (Fig. 29G-H), a species of Pisaniidae (Buccinoidea) whose shell morphology and (particularly) colouration is strangely reminiscent of the type species, *L. parva*.

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Table 2. List of the valid extant taxa in ERGALATAXINAE

Bold: new taxa described in this paper.
Asterisk: taxa sequenced in Claremont et al. (2013) or in this paper.
Question mark: doubtful classification after sequencing, but a temporary placement in the genera in which they are currently assigned is suggested.
NC: New combination.

Genus	Type species	Species	
Azumamorula Emerson, 1968	*Ricinula mutica* Lamarck, 1816	*A. mutica* (Lamarck, 1816)	
**Bedevina* Habe, 1946	*Trophon bireleffi* Lischke, 1871	**B. bireleffi* (Lischke, 1871)	
***Claremontiella* n. gen.**	*Purpura nodulosa* C.B. Adams, 1845	***C. adiakritos* n. sp.**	
		C. consanguínea (E.A. Smith, 1891)	**NC**
		**C. nodulosa* (C.B. Adams, 1845)	**NC**
**Cronia* H. & A. Adams, 1835	*Purpura amygdala* Kiener, 1835	**C. amygdala* (Kiener, 1835)	
		**C. aurantiaca* (Hombron & Jacquinot, 1853) (see note)	
		C. avellana (Reeve, 1846)	
**Cytharomorula* Kuroda, 1953	*Cytharomorula vexillum* Kuroda, 1953	***Cytharomorula absidata* n. sp.** [(as *Cytharomorula* cf. *grayi* in Claremont et al. (2013)]	
		C. ambonensis Houart, 1996	
		***C. arta* n. sp.**	
		C. benedicta (Melvill & Standen, 1895)	
		C. danigoi Houart, 1995	
		C. dollfusi (Lamy, 1938)	
		***C. elegantula* n. sp.**	
		***C. fatuhivaensis* n. sp.**	
		**C. grayi* (Dall, 1889)	
		C. lefevreiana (Tapparone Canefri, 1880)	
		***C. manusuduirauti* n. sp.**	
		**C. ornamentata* (Houart, 1995)	**NC**
		**C. paucimaculata* (Sowerby, 1903)	
		C. pinguis Houart, 1995	
		**C. springsteeni* Houart, 1995	
		**C. vexillum* Kuroda, 1953	
Daphnellopsis Schepman, 1913	*Daphnellopsis lamellosa* Schepman, 1913	*D. fimbriata* (Hinds, 1843)	
		D. hypselos Houart, 1995	
		D. lamellosa Schepman, 1913	
		D. lochi Houart, 2013	
		D. lozoueti Houart, 2013	
		D. pinedai Houart, 2013	
**Drupella* Thiele, 1925	*Drupa cornus* Röding, 1798	**D. cornus* (Röding, 1798)	
		**D. eburnea* (Küster, 1862)	
		**D. fragum* (Blainville, 1832)	
		**D. margariticola* (Broderip, 1833)	
		D. minuta Fujioka, 1984	
		**D. rugosa* (Born, 1778)	
**Ergalatax* Iredale, 1931	*Ergalatax recurrens* Iredale, 1931 = *Murex pauper* Watson, 1883	**E. contracta* (Reeve, 1846)	
		E. crassulnata (Hedley, 1915)	
		E. dattilioi Houart, 1998	
		E. heptagonalis (Reeve, 1846)	
		**E. junionae* Houart, 2008	
		E. martensi (Schepman, 1892)	
		E. pauper (Watson, 1883)	
		E. tokugawai Kuroda & Habe, 1971	
		E. zebra Houart, 1995	

Table 2 (continued)

Genus	Type species	Species	NC
**Lataxiena* Jousseaume, 1883	*Lataxiena lataxiena* Jousseaume, 1883 = *Trophon fimbriatus* Hinds, 1844	*L. blosvillei* (Deshayes, 1832) *L. bombayana* (Melvill, 1893) *L. cumella* (Jousseaume, 1898) *L. desserti* Houart, 1995 **L. fimbriata* (Hinds,1844) *L. habropenos* Houart, 1995 *L. lutescena* Zhang & Zhang, 2015 *L. solenosteiroides* Houart, Fraussen & Barbier, 2013	
***Lauta* n. gen.**	*Ricinula parva* Reeve, 1846	**L. parva* (Reeve, 1846)	**NC**
Lindapterys Petuch, 1987	*Lindapterys vokesae* Petuch, 1987 (early Miocene, Florida)	*L. domlamyi* Garrigues & Merle, 2014 *L. murex* (Hedley, 1922) *L. sanderi* Petuch, 1987 *L. soderiae* Callea, Volpi, Martignoni & Borri, 2001	
**Maculotriton* Dall, 1904	*Triton bracteatus* Hinds, 1844 = *Buccinum serriale* Deshayes, 1834	**M. serriale* (Deshayes, 1834)	
**Morula* s.s. Schumacher, 1817	*Drupa uva* Röding, 1798	*M.* (*M.*) *albanigra* Houart, 2002 *M.* (*M.*) *angulata* (Sowerby, 1893) **M.* (*M.*) *aspera* (Lamarck, 1816) (see note) *M.* (*M.*) *cernohorskyi* Houart & Tröndlé, 1997 **M.* (*M.*) *chrysostoma* (Deshayes, 1844) **M.* (*M.*) *echinata* (Reeve, 1846) **M.* (*M.*) *nodicostata* (Pease, 1868) *M.* (*M.*) *oparensis* (Melvill, 1912) *M.* (*M.*) *peasei* Houart, 2002 *M.* (*M.*) *praecipua* Rehder, 1980 *M.* (*M.*) *rodgersi* Houart, 2000 **M.* (*M.*) *uva* (Röding, 1798) *M.* (*M.*) *variabilis* (Pease, 1868) **M.* (*M.*) *zebrina* Houart, 2004	
**Morula* (*Habromorula*) Houart, 1995	*Purpura biconica* Blainville, 1832	*M.* (*H.*) *aglaos* (Houart, 1995) *M.* (*H.*) *ambrosia* (Houart, 1995) *M.* (*H.*) *bicatenata* (Reeve, 1846) **M.* (*H.*) *biconica* (Blainville, 1832) **M.* (*H.*) *coronata* (H. Adams, 1869) *M.* (*H.*) *dichrous* (Tapparone Canefri, 1880) *M.* (*H.*) *euryspira* (Houart, 1995) *M.* (*H.*) *fuscoimbricata* (Sowerby, 1915) **M.* (*H.*) *japonica* (Sowerby, 1903) *M.* (*H.*) *lepida* (Houart, 1995) *M.* (*H.*) *porphyrostoma* (Reeve, 1846) **M.* (*H.*) *spinosa* (H.& A. Adams, 1853) **M.* (*H.*) *striata* (Pease, 1868) *M.* (*H.*) *whiteheadae* Houart, 2004	
***Murichorda* n. gen.**	*Murex fiscellum* Gmelin, 1791	**M. fiscella* (Gmelin, 1791) *M. jacobsoni* Emerson & D'Attilio, 1981 **M. rumphiusi* Houart, 1996	**NC** **NC** **NC**
**Muricodrupa* Iredale, 1918	*Purpura fenestrata* Blainvville, 1832)	**M. anaxares* (Kiener, 1835) **M. fenestrata* (Blainville, 1832)	**NC**
**Oppomorus* Iredale, 1937	*Purpura nodulifera* Menke, 1829	**O. funiculatus* (Reeve, 1846) **O. noduliferus* (Menke, 1829) **O. purpureocinctus* (Preston, 1909)	

Table 2 (continued)

Genus	Type species	Species	NC
Orania* Pallary, 1900 **Note: Type species not analysed in Claremont et al. (2013)	*Murex spadae* Libassi, 1859 = *Murex fusulus* Brocchi, 1814	*O. adiastolos* Houart, 1995	
		O. archaea archaea Houart, 1995	
		O. archaea hitomiae Houart & Moe, 2011	
		O. atea Houart & Tröndlé, 2008	
		O. badia (Reeve, 1845)	
		* ?*O. bimucronata* (Reeve, 1846)	
		**O. carnicolor* (Bozzetti, 2009)	NC
		**O. castanea* (Küster, 1886)	
		O. corallina (Melvill & Standen, 1903)	
		O. dharmai Houart, 1995	
		O. ficula (Reeve 1848)	
		**O. fischeriana* (Tapparone-Canefri, 1882)	
		O. fusulus (Brocchi, 1814)	
		* ?*O. gaskelli* (Melvill, 1891)	
		O. livida (Reeve, 1846)	
		O. maestratii Houart & Tröndlé, 2008	
		**O. mixta* Houart, 1995	
		O. nodosa (Hombron & Jacquinot, 1841)	
		O. nodulosa (Pease, 1869)	
		O. pachyrhaphe (Smith, 1879)	
		**O. pacifica* (Nakayama, 1988)	
		O. pholidata Watson, 1883	
		O. pleurotomoides (Reeve, 1845)	
		***O. pseudopacifica* n. sp.**	
		O. purpurea (Kuroda & Habe, 1961)	
		O. rosadoi Houart, 1998	
		**O. rosea* Houart, 1996	
		* ?*O. serotina* (A. Adams, 1853)	
		O. simonetae Houart, 1995	
		O. subnodulosa (Melvill, 1893)	
		O. taeniata Houart, 1995	
		O. taiwana (Lai & Jung, 2012)	NC
		O. walkeri (Sowerby, 1908)	
		O. xuthedra (Melvill, 1893)	
Pascula* Dall, 1908 **Note: Type species not analysed in Claremont et al. (2013)	*Trophon citricus* Dall, 1908	*P. citrica* (Dall, 1908)	
		**P. darrosensis* (E.A. Smith, 1884)	
		**P. muricata* (Reeve, 1846)	
		**P. ochrostoma* (Blainville, 1832)	
		P. ozenneana (Crosse, 1861)	
		P. palmeri (Powell, 1967)	NC
		P. philpoppei Houart, 2018	
		P. rufonotata (Carpenter, 1864)	
		**P. submissa* (E. A. Smith, 1903)	
**Phrygiomurex* Dall, 1904	*Triton sculptilis* Reeve, 1844	**P. sculptilis* (Reeve, 1844)	
**Spinidrupa* Habe & Kosuge, 1966	*Murex euracanthus* A. Adams, 1853	*S. aethes* Houart, 2017	
		* *S. euracantha* (A. Adams, 1853)	
		* ?*S. infans* (E.A. Smith, 1884)	
**Tenguella* Arakawa, 1965	*Purpura granulata* Duclos, 1832	**Tenguella ceylonica* (Dall, 1923)	
		***T. chinoi* n. sp.** [as *Tenguella* n. sp. in Claremont et al (2013)]	
		***T. ericius* n. sp.**	
		**T. granulata* (Duclos, 1832)	
		T. hoffmani Houart, 2017	
		**T. marginalba* (Blainville, 1832)	
		**T. musiva* (Kiener, 1835)	

Table 2 (continued)

Genus	Type species	Species	NC
**Trachypollia* Woodring, 1928	*Trachypollia sclera* Woodring, 1928	*T. didyma* (Schwengel, 1943) **T. lugubris* (C.B. Adams, 1852) *T. sclera* (Woodring, 1928) *T. turricula* (Maltzan, 1884)	
**Usilla* H. Adams, 1861	*Vexilla nigro-fusca* Pease, 1860 = *Vexilla fusconigra* Pease, 1860 = *Purpura avenacea* Lesson, 1842	**T. avenacea* (Lesson, 1842)	
Uttleya Marwick, 1934	*Uttleya arcana* Marwick, 1934 (lower Pleistocene, New Zealand)	*U. ahiparana* (Powell, 1927) *U. marwicki* Powell, 1952 *U. williamsi* Powell, 1952	

Note: Small genetic distances are suggestive of possible synonymy of species; for example, there was < 1% divergence among COI sequences for the pair *Morula uva* and *M. aspera*, and similarly for the pair *Cronia amygdala* and *C. aurantiaca* (Claremont et al., 2013).

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